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BY

DR. ALLEN THOMSON.

1855

(*From the Cyclopædia of Anatomy and Physiology.*)

OVUM. — In Animal Anatomy and Physiology, the Egg, the product of parental sexual generation, from which the young of animals are produced.

The Functions of Reproduction, as observed in the higher orders of animals and in the human species, are generally divided into two classes of processes; the one of which comprehends those operations by which the parents contribute to the production of the germs from which the young are formed; the other, those processes or changes which occur more immediately in the product of generation itself, and which relate to the formation or development of the new being from a germ or ovum. In the Article GENERATION of this Cyclopædia, the functions belonging to the first of these divisions have been described; and it is proposed in the present Article to treat of the second class of reproductive phenomena, or those which relate more immediately to the origin, formation, and growth of the new being, and which are usually described under the titles of Ovology, Embryology, and Fœtal Development.

In this, as in the former article, the history of the functions as they occur in the human species will receive the greatest share of our attention; but in describing the process of development of the young, still more than in the history of the functions of the parents that are preliminary to the production of a perfect germ, it is necessary to extend our observations to the various members of the animal kingdom, and even in some degree also to plants, from which, as much as from direct observations or experiments in man, has been derived our knowledge of the individual facts and of the general laws relating to the process of embryonic development.

The arrangement followed in that part of the article which treats of Development will be adapted more immediately to the consideration of human reproduction; and the statements in regard to animals, or to organised beings in general, will be made chiefly subordinate to, or illustrative of, the functions in the human species; but the facts in human and comparative embryology are so intimately connected, that it will be expedient to incorporate with the article such a description of the formative process in different animals as may present a sketch of the general nature of this interesting process in the whole animal kingdom.*

In pursuing this plan, the topics to be discussed may be arranged under the following heads: viz. —

1st. Nature of the Ovum in general, with reference to the different forms of the reproductive function in various animals.

2nd. The structure, properties, mode of origin, and formation of the Ovum.

3rd. The changes which the ovum undergoes in the process of Fecundation, and (in so far as the ovum itself is concerned) the circumstances which influence that process.

4th. The external circumstances which influence the development of the ovum and embryo, especially Incubation and Utero-gestation.

5th. The Phenomena of Fœtal Development in general, and the history of the origin and development of each system, organ, and texture of the body in particular.

6th. The Functions of the Embryo or Fœtus as compared with those of the adult.

The wide-spread importance of embryological anatomy and physiology is now so generally acknowledged by all who have made them a subject of study, that to them no apology is required for the length of this treatise. To those who have not made them an object of their special attention, it will be enough at this place to advert to the extensive range of topics which must be embraced in an attempt to trace the history of the first origin and subsequent evolution of all the parts of so complex and various a structure as the body of animals; and to remind them that this department of science professes to describe not merely the successive changes of external form and relation by which the several organs, springing from imperceptible beginnings, arrive at their perfect condition, but also the more minute phenomena of histological development, or changes of the several textures, which accompany the more obvious formative processes; that, as in many instances the complete knowledge of the structure and function of an organ is only to be obtained by the observation of its fœtal conditions, the study of development is accessory or supplementary to many departments of anatomy and physiology; that, in recent times, no branch of inquiry relating to organic nature has made more rapid progress, has presented a greater amount of new discoveries, or has influenced in a greater degree the views of scientific men on allied subjects, than the science of embryology; that it is coextensive with, and illustrative of, the whole range of comparative anatomy; that no system, therefore, of zoological classification can be regarded as philosophical or complete which neglects the facts and principles of fœtal development: finally, that some departments of pathological anatomy receive considerable illustration from our science, and that more especially the scientific study and comprehension of teratology or congenital malformations is founded entirely on an accurate knowledge of the phenomena and laws of development. Our subject, therefore, is not only interesting by itself, but deeply important as an essential branch of philosophical anatomy and physiology.*

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* It was originally intended to have treated in the same article of the embryology of plants; but the extent and importance of that subject in connection with general physiology makes it necessary to postpone its consideration to a separate article, under the head of VEGETABLE OVUM.

Before proceeding with the particular history of the ovum, and its development in man and the higher animals, which will form the greater part of the following article, some topics of a general and preliminary nature present themselves for our consideration.

The investigation of the process of reproduction in the lower animals has made so much progress during the last few years, that it becomes necessary to place before the reader a sketch of the aspect in which more modern researches enable the physiologist to view the relation of the ovum to the sexual generative function, and to the other means by which individuals are multiplied, or species are reproduced in the whole animal kingdom. In the Article Generation, the commonly received distinction was drawn between the sexual and the non-sexual modes of generation; and under the latter form a variety of processes of Gemmation and Division were alluded to as occasional or constant substitutes in a certain number of animals for the more permanent sexual form of the reproductive process. At the time of the publication of that article, the sexual organs had not been discovered in a considerable number of the lower animals: but since then, the assiduous and accurate researches of embryologists have gradually diminished the number of animals so situated, by bringing to light the male and female reproductive organs, or their essential products, in nearly every species of the animal kingdom; so that now only a very few, and those of the simplest organisation, remain, in which the bisexual condition has not been detected. These animals belong exclusively to the division of the animal kingdom recently established by Zoologists, as Protozoa, comprehending the Polygastric Infusoria, Rhizopoda and Porifera.*

In all other animals it is now ascertained that fecundated ova, formed by an act of sexual generation, are the means of securing the permanent reproduction of the species; but in several of them, as is especially well known among the Polypine tribes, a vast multiplication of individuals, sometimes living separately, but more frequently associated in groups, or living in united colonies, takes place by a non-sexual process of reproduction, which may be compared in many instances to the growth or repetition of the parts of a tree or plant by budding.

Recent investigations have made it more and more apparent, that the non-sexual multiplication of animals ought to be distinguished into several kinds, according to the different circumstances in which it may occur. In a few, as already remarked, it is entirely without known sex: in others, the non-sexual process of gemmation, or division, gives rise to new individuals, which are simply the repetitions of the perfect or complete animals; and in a third set, the non-sexual multiplication occurs more frequently in an incomplete condition of the animal, and often consists in the production of one or more series of dissimilar forms of animals, the last generation of which alone becomes sexually complete, and propagates the species by fecundated ova. This constitutes the variety of the reproductive process recently distinguished by the name of Alternating Generation.

Three forms, therefore, of non-sexual animal reproduction, or multiplication, are to be distinguished from the sexual mode of generation, as in the following enumeration:—

I. True sexual generation, direct or indirect, in all animals, excepting the Protozoa.

II. Non-sexual multiplication, occurring only in some of the invertebrated animals;

1st. In Protozoa, in which sexual organs have not yet been discovered.

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* A variety of circumstances have contributed to cause delay in the appearance of the present article, some of them of a nature beyond the control of the author. He is sensible, however, that an apology is due by him to the readers of this work on account of the protraction of that delay. He has only to say, that in the contemplation of the vastness and imperfectly known condition of the subject, he has ever felt more disposed to engage in the investigation of some of its details, than to appear before the public as a systematic writer in regard to it. The delay may have this advantage, however, that it will enable him to introduce a greater number of new discoveries, a more accurate statement of individual facts, and more correct and extended general views of the subject than might have been possible at an earlier period, and that it will afford him an opportunity of correcting and amplifying various statements contained in the previous Article Generation, which the progress of discovery since the time of its publication has rendered necessary.

* The first two of these divisions may be described as simple unicellular microscopic animalcules, the third rather as a compound or congeries of microscopic animalcules: the Porifera, or Sponges, are included in this division of Protozoa, because the balance of evidence is decidedly in favour of their animal nature.

2nd. In Animals known to be capable of sexual generation; including two varieties, viz.

a. Multiplication of similar individuals, either in a mature or immature condition.

b. Multiplication of individuals, generally dissimilar from those producing them, and becoming at last mature or complete in the exercise of the true generative function.

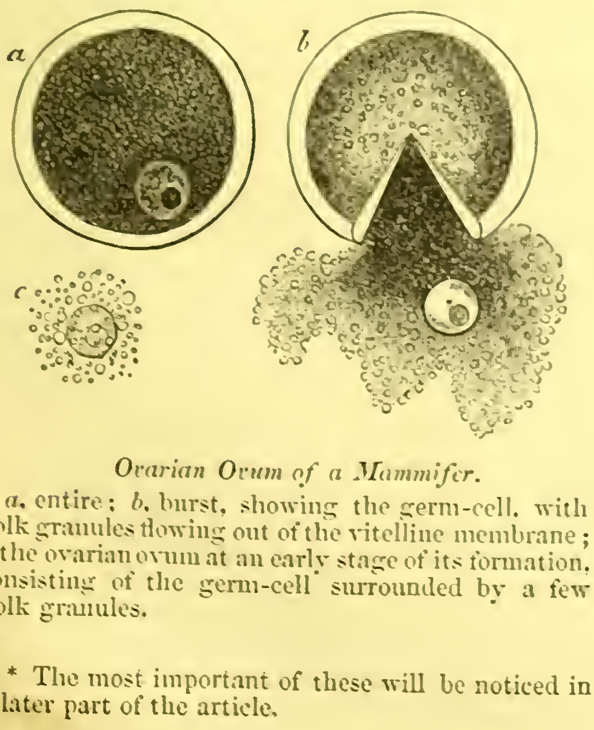
Some account of these various forms of the reproductive process, and especially of the last, as established by recent discovery, supplementary to that contained in the Article GENERATION, may be introduced here, with a view to serve as a foundation for general views of the nature of the ovum, and its relation to the reproductive process in general.

I. OF THE OVUM IN GENERAL, AS RELATED TO THE SEXUAL PROCESS OF GENERATION.

The term *ovum* is in this article entirely restricted to the product of sexual generation. This body is formed in the ovary of the female parent (or in the female organ of a hermaphrodite parent) by a gradual process of growth or development. When it arrives at a state of maturity, it is spontaneously discharged from the place of its formation, a process which in the higher animals has received the name of *Ovulation.* If left to its own unassisted powers, no organic change of importance follows in the ovum, and it remains incapable of producing an embryo. But if, at or near the time when the ovum, in a state of maturity, leaves the ovary, it be subjected to the influence of the male product or sperm by the contact of a very minute portion of that substance, it then undergoes the change of Fecundation, by which it has communicated to it the power of having developed within it a new being specifically resembling its parents.

Although there are many great apparent differences in the form and structure of the ova of animals*, yet a general comparison of their organisation shows that they consist in nearly all of parts that are essentially the same. These parts in the ovarian ovum are the following, beginning with that which appears most essential: 1st, The *Germinal Vesicle*, or *Germ-cell;* a nucleated organic cell of microscopic size, generally situated near the surface of the ripe ovarian ovum; this is embedded superficially in, 2nd, The *Vitellus*, *Yelk*, or *Yolk*, a mass of oleo-albuminous matter, partly fluid, and partly cellular and granular, generally of proportionally much greater size than the germ-cell, and serving to furnish materials for the changes of that body, and for the development of the new being. Both of these parts are enclosed by, 3rd, The *Vitelline*, or *Yolk-Membrane*, a vesicular, nearly structureless, membrane, which contains the rest, and gives to the whole usually more or less of a spherical form. To the assemblage of these parts, constituting the ovarian ovum, and which may be looked upon as most immediately important in connection with the formative process, there are generally added, after it has left the ovary, and in the progress of its descent through the female passages, some others, such as the albumen, outer membrane and shell of the bird's egg. In their simplest form these additional parts constitute an external covering of the egg, to which the name of *Chorion* is often applied.

Fig. 1.

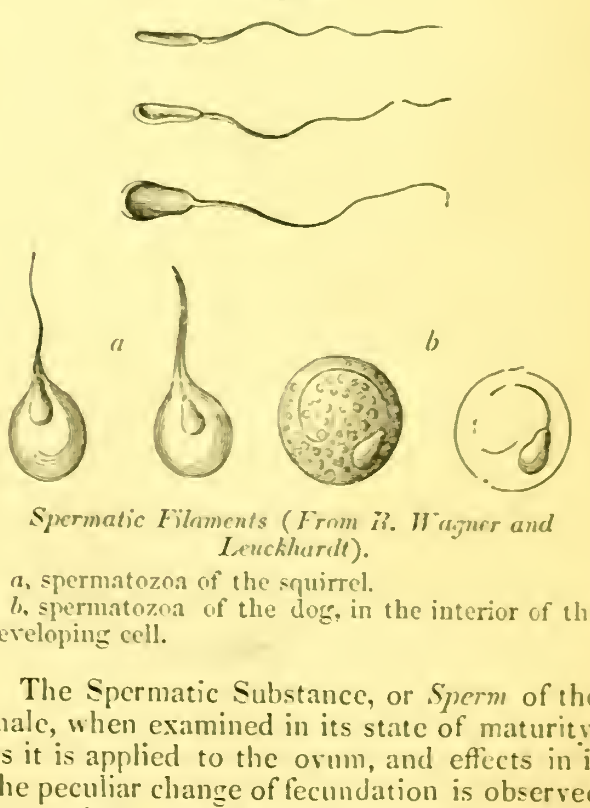


Ovarian Ovum of a Mammifer.

a, entire; *b*, burst, showing the germ-cell, with yolk granules flowing out of the vitelline membrane; *c*, the ovarian ovum at an early stage of its formation, consisting of the germ-cell surrounded by a few yolk granules.

If the ovum be traced back to its earliest origin in the ovary, it is found to consist at first of the germinal vesicle, germ-cell or its nucleus (*fig.* 1, c.). To this cell the substance of the yolk is added in the progress of its formation, generally in a gradual manner, but in some animals more suddenly.

Fig. 2.



Spermatic Filaments (From R. Wagner and Leuckhardt).

a, spermatozoa of the squirrel.
b, spermatozoa of the dog, in the interior of the developing cell.

The Spermatic Substance, or *Sperm* of the male, when examined in its state of maturity, as it is applied to the ovum, and effects in it the peculiar change of fecundation is observed to consist essentially of an immense number of minute bodies, generally consisting of a thicker particle, with a fine filament attached, and almost always exhibiting, when recently mixed with water, vivid vibratory or undulatory movements, but in a few animals presenting other forms, and without motion. These spermatic filaments or particles are developed by a peculiar process in the interior of the cells (*sperm-cells*) secreted in the male organ or testis.

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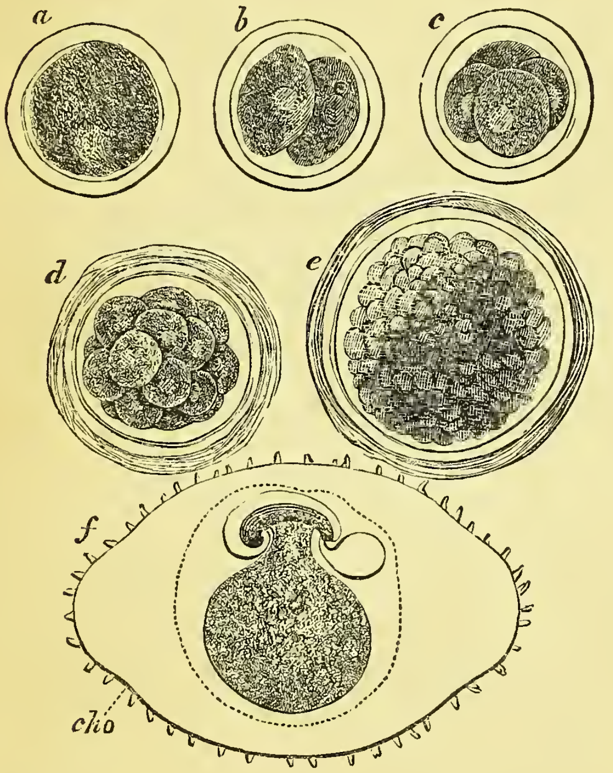
* The most important of these will be noticed in a later part of the article.

When the ovarian ovum has arrived at maturity, the germ cell disappears as such, and if fecundation shall have taken place, that vesicle is succeeded by another minute cell, with which the origin and development of the new animal are most intimately associated. This secondary organic cell of the fecundated ovum has therefore been called the *Embryo-cell.* The first changes, preparatory to the commencement of the development of an embryo, consist in the formation out of the embryo-cell and yolk substance of an organised cellular mass, or of a membranous covering of the whole or a part of the yolk: this is the *germ-mass*, *Blastoderm*, or *germinal membrane.*

Fig. 3.



Fecundated Ovum of a Mammifer, with the Embryo Cell and its division.

a, ovum with the first embryo-cell ; *b*, division of embryo-cell and cleavage of the yolk round it ; *c*, second division and cleavage ; *d*, farther division ; and *e*, germ-mass or Blastoderm forming ; *f*, diagram of the embryo with its membranes, the amnion, allantois, &c., within the chorion.

The process by which this primary organised part is produced varies somewhat in different animals; but it appears to consist in a multiplication of the embryo-cell by changes of the nature of cytogenesis, accompanied with more or less of a cleavage or sub-division of the substance of the yolk, and its combination with the progeny of the embryo-cell. The general result is, that the first rudiments of the new being take their origin in organic cells, which are descended from the original embryo-cell.

From this blastodermic mass or membrane, the embryo, or fœtus, or new animal, and in the higher animals some accessory parts, which are temporarily united with the embryo previous to its birth, originate, and are gradually formed, by a various process of progressive organic growth of an epigenetic character, which is termed *Development, or Embryo-genesis.*

In by far the greater number of animals an ovum gives rise to only one embryo or individual, and this one becomes by itself, when its growth is complete, the perfect sexual animal, capable of contributing its share to the production of fecundated ova. But in a certain number of animals, to which allusion will be made more fully afterwards, the immediate product of development from the ovum is not at once, and by itself, converted into a complete sexual individual ; but by an intermediate non-sexual process of production, one or more new individuals are formed out of the body of that first developed, and to the last so formed is committed the office of sexual reproduction, or true generation.

The essential conditions and phenomena, therefore, of the sexual process of generation, as related to the ovum, and as limited by the foregoing considerations, may be shortly stated to be the following :—

1st. The formation of the ovarian ovum of the female sex, containing the germ-cell.

2nd. The formation of the sperm-cells of the male sex, and the development of their peculiar spermatic elements.

3rd. The mutual action of these two products in the fecundation of the ovum.

4th. The disappearance of the germ-cell of the ovarian ovum, and the formation of the embryo-cell in the fecundated egg.

5th. The multiplication of the embryo-cell by cytogenesis, and the formation from that body, and from the yolk, or a part of it, of the blastodermic mass or membrane.

6th. The process of embryo-genesis, or development of the systems, organs, and textures of the new animal.

It is right to state that the original germ-cell has not yet been ascertained to exist in the ovum of every animal, nor has its successor, the embryo-cell, been observed in all instances ; but they have been detected in so very large a proportion, that it appears extremely probable that in all sexual animals the generative process consists in the process above described, or in some modification of it. I refrain at present from farther details as to these phenomena, and have stated the results only in their most general form, because I shall have occasion to return upon some of them in a subsequent part of the article. Looking back on this general statement of the commencement and progress of the genetic process in animals, it will be seen that the new being may be considered as taking its immediate origin from the progeny of cells descended from the embryo-cell. That cell appears with great probability to take its origin from the germ-cell, or its nucleus, or from some part of it, in combination with a determinate portion of the sperm product, or descendent of the sperm-cell; and we are so far justified, therefore, in ascribing the genetic process by which the new being is formed to the mutual action of the products of two different kinds of cells, viz., the germ-cell and the sperm-cell.*

In conclusion, the ovum may be defined to be a distinct vesicular body originally formed from a cell, presenting throughout its existence the organic cellular structure, consisting of oleo-albuminous materials, formed by the female of an animal species, and capable, when acted on by the spermatic product of the male, of undergoing the successive changes of embryo-genesis, by which, either directly or through intervening generations, the species of animals is reproduced and continued.

The structural distinctive characters of an ovum are, therefore, its enclosure within a distinct vesicular covering, and its original organic cellular constitution in the germ-cell: its most important physiological characteristic is its susceptibility of the changes of embryonic development under the influence of the sperm-cell or its product.

II. Of the non-sexual Mode of Generation.

The necessity of distinguishing several kinds of non-sexual reproduction according to its occurrence in animals entirely without sex, or believed to be so, and in those which may also be propagated in the sexual mode, has already been adverted to. A farther distinction of the non-sexual reproduction may be made according to the nature of the process itself: thus, some forms of it consist in the development of buds, so intimately united with the parent substance, that scarcely any difference can be perceived between their mode of formation and that of continuous growth, as in Hydra and various Polypes: other forms consist in the development of new individuals from germs so isolated in their form and cellular in their structure, that it might seem at first sight arbitrary to distinguish them from ova, as in Aphides; others appear to hold an intermediate place and character between these two forms, as in Salpa: while, in a fourth set, a more complex and varied series of changes occurs, which may be regarded with probability as modifications of the gemmal or germinal processes, as in Medusoid Polypi, Taenia, &c. But it will be apparent from what follows that we are as yet very far from that exact knowledge of the nature and first origin of buds, gemmae, or other kinds of germs, from which animals may be multiplied in the non-sexual modes, which would enable us to form satisfactory general conclusions as to their mutual relations, and their similarity or difference, as compared on the one hand with organic growth, and on the other with oval development.

As the accurate determination of these relations is in a great measure impossible, it will be expedient for the present to state only very briefly the general characters of the several non-sexual modes of reproduction, before selecting for more particular consideration some varieties of the process, the recent investigation of which seems calculated to influence in a considerable degree future general views of the whole subject of reproduction. We shall also defer for the present any minute consideration of the relation of these processes to the growth or development of cells, for we shall have occasion to treat more at length of that subject in a subsequent part of this article, and in that of vegetable ovum.*

At this place it is only necessary to remind the reader, that all processes of development, whether in the earliest or at more advanced stages of formation, appear to consist essentially in, or are more or less intimately connected with, a multiplication of organic cells in the parts that are developed. In the unicellular beings, fissiparous and gemmiparous multiplication may easily be recognised to be processes of cell growth; the one consisting in the division of the parent cell into a progeny of two by a nearly equal partition of its substance; the other, in an extension and gradual enlargement of a small or limited portion of the original cell. But in many of the instances of fission and gemmation on the larger scale with which we are acquainted, observation has not yet pointed out the primary cell, if it exists, from which the process of division or extension begins; and, indeed, most instances of fissiparous division may, as Dr. Carpenter has remarked, be referred to a peculiar modification of gemmation.

The process of budding or gemmation is usually stated to occur in one of two modes. 1st, by the extension of a part of the parent body which remains in organic connection with it during the development of the new individual from the bud; the attached bud either sprouting from the exterior, or being developed in the interior of the parent stock. 2nd, by the development of the new individual from a small detached portion of the substance of the parent, which undergoes the principal formative changes after its separation. These separate buds have been called gemmae, gemmules, bulbils, &c., and two kinds of them may also be distinguished according as they are thrown off from the external surface of the parent body, or are formed and become loose within its interior. These gemmules have frequently attained to some degree of development by the time of their separation, and very often are provided with cilia over their surface, which cause them to move rapidly through fluids. From the first they exhibit a minutely cellular and granular structure: but it does not appear that they are originally formed from any single nucleated cell: they appear rather from the first to be a congeries of cell progenies. They are destitute of an external envelope; but, nevertheless, it may often be difficult to distinguish between them and true ova.

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* These views have been stated with great clearness by Prof. Owen in his various writings, especially in his Essay on Parthenogenesis, and Lectures on Generation, &c., in Medical Times, 1849, and by Dr. Carpenter in his Principles of Physiology, General and Comparative. 1851.

* For a very lucid and agreeable statement of these relations the reader is referred to Dr. Carpenter's able Treatise on General and Comparative Physiology. 1851.

The tendency to the multiplication of individuals by non-sexual reproduction is greatest among those animals which are of the simplest organisation, and more especially among those in which the cellular structure predominates; not that it is confined to them, nor that it occurs in all animals so constituted, but that it is much more frequent and complete in the simplest animals of each class in which it has been observed; as if it were more liable to occur in those species in which the process of individual development had proceeded to the least extent of advancement in the formation of the living textures of their bodies. There is accordingly a remarkable similarity in the nature of the processes of non-sexual multiplication and ordinary growth in these very simple animals; and it is well known that the same relation subsists between a low organisation of animals, and their disposition or power to repair individual parts of their bodies lost by injury or accident.[*]

1st. *Of the Process of Reproduction in Protozoa, or animals in which the sexual distinction has not yet been discovered.*

Among the Protozoa reproduction takes place in two modes, viz., 1st, by the process of gemmation or fission, and, 2nd, by development from separated gemmules or germs. For an account of the first of these processes, the reader is referred to the articles POLYGASTRIA and PORIFERA.[†]

Among the Polygastria multiplication by division is much more frequent than that by gemmation. It consists in the fission or division of the whole unicellular body into two nearly equal parts, each of which becomes, when separate, a perfect animalcule like the original one: in some the division is transverse, in others longitudinal, and occasionally it occurs in either of these modes in different individuals of the same species. The nucleus of the unicellular polygastria has been frequently observed to undergo division previous to the formation of the fissure, by which the division of the external wall is completed,—a fact which has led some physiologists, as Ehrenberg, M. Barry, and Owen, to attribute to the nucleus an important influence in this process of cleavage; the first of these observers having even conceived the nucleus to act the part of a male or fecundating organ. This latter view is not, however, adopted by many of those who have made a study of this class of animals.

In some of the polygastria in which the process of multiplication is either of a fissiparous or gemmiparous kind, as in Vorticella, Uvella, and Polythalamous Rhizopoda, the new individuals remain in connection, and are associated together in branched pediculated groups, in connected masses of a globular form, or in regular spiral united series.[*]

The Porifera, or sponges, appear to be reproduced by a different kind of gemmation from that now described in polygastria,—viz., by separate gemmules or small portions of the substance of the sponge, which, soon after having been detached from the main stock, are moulded into a spherical form, and, being provided with cilia, move about in the water with great vivacity for a considerable period. These gemmules are thrown off in numbers proportional in some measure to the activity of the nutrition of the sponge, and therefore principally during the early part of summer. Towards the approach of winter a different kind of reproductive bodies is observed to be formed,—viz. small capsules containing globular germs, which, after development within the capsule, pass out of it and produce a new sponge for every capsule or germ. These bodies have been called ova, and certainly they bear very great resemblance to them; but too little is known of their nature and origin to enable us to form an opinion whether they are to be regarded as precisely of the same nature as ova or not. In the mean time they may be named the capsular germs.[†]

But it appears that, among the polygastria, and rhizopoda also, there are sometimes formed, by a peculiar process not ascertained to be of a sexual kind, minute reproductive bodies of a cellular structure, which, if they are not true ova, are at least substitutes for them.[‡]

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[*] See Mr. Paget's recent interesting lectures on this subject, published in Medical Gazette, 1849.

[†] A considerable number of the polygastric infusoria described by Ehrenberg in his great work on that class, are now very generally regarded as belonging to the vegetable rather than to the animal kingdom, such as the families Closterina, Volvocina, and Bacillaria.

[*] See an interesting paper by Dr. Carpenter on the Genus Nummulina and other Foraminifera in Quart. Journ. of Geol. Soc. Feb. 1850. Some judicious and interesting remarks on this class of animals, and on the relations and characters of the Protozoa in general, are contained in a recent paper by Mr. Huxley in the Annals of Natural History (1851, vol. viii. p. 437.), in which he has described a curious monocellular genus named Thalassicolla, which occurs in masses, and forms spicula somewhat like a minute sponge.

[†] See Laurent's elegant memoir, Recherches sur l'Hydre et l'Eponge d'eau douce. 1842.

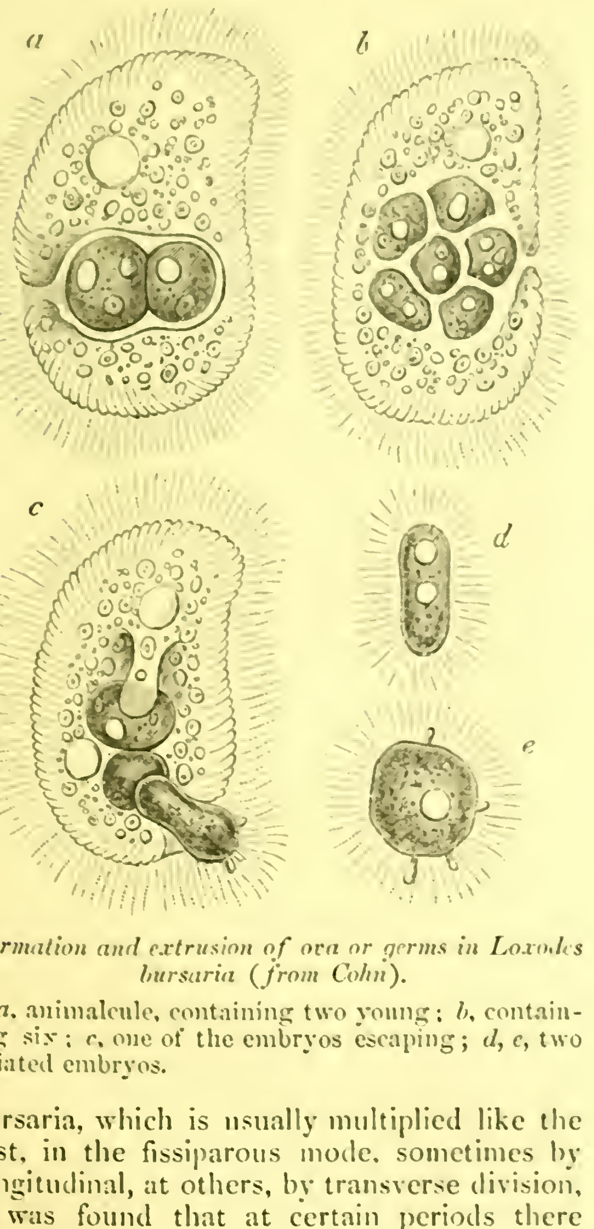
[‡] Allusion is not made here to the production of granules by the diffluence of an infusorian animalcule erroneously taken by Ehrenberg for the deposition of ova, but to a very different process. Dujardin, who pointed out this error (Hist. Nat. des Infusoires, p. 101.), is of opinion that, besides the processes of fission and gemmation, we know nothing with certainty of the reproduction of infusoria; but he admits that it is possible that the minute bodies into which an infusorian breaks up by diffluence might prove the germs of new individuals. Dr. Carpenter has mentioned several instances of a kind similar to those alluded to in the text, and has expressed the opinion that something of the nature of sexual production may yet be discovered to take place in these animals (Prin. of Gen. and Comp. Physiol. p. 249, and p. 917.). Observations of a similar kind are re-

Some recent observations appear to throw additional light on this subject, and to make it probable that in some circumstances this process is in some sort analogous, or at least equivalent, to one of sexual reproduction.

The first accurate observation of the development of a progeny of young cells within the body of a polygastrian was communicated by Focke in 1844 to the meeting of naturalists at Bremen, and the fact of the production of internal germs or bodies resembling ova or spores within the body of these animalcules has recently received full confirmation from the observations of Stein and of Cohn.*

In Cohn's observations, which were made on a paramaecian polygastrian, the Loxodes bursaria, which is usually multiplied like the rest, in the fissiparous mode, sometimes by longitudinal, at others, by transverse division, it was found that at certain periods there were formed within the bodies finely granular colourless cells, in some only one, more frequently several, and occasionally as many as six or seven, nearly of a uniform size, and each presenting two contractile vesicles like the parent. The escape of these bodies, by their passage through an aperture temporarily formed in the wall of the infusorian, was carefully observed; the exit of each embryo occupied about twenty minutes. Soon after their escape they exhibited active ciliary motion, and moved about with all the appearance of embryo-infusoria. Although the farther development of these bodies was not traced, the observations on this animal, and on another, the Urostyla grandis, afford sufficient proof that the infusoria may be propagated by minute separate germs, as well as by division of their bodies.

Fig. 4.



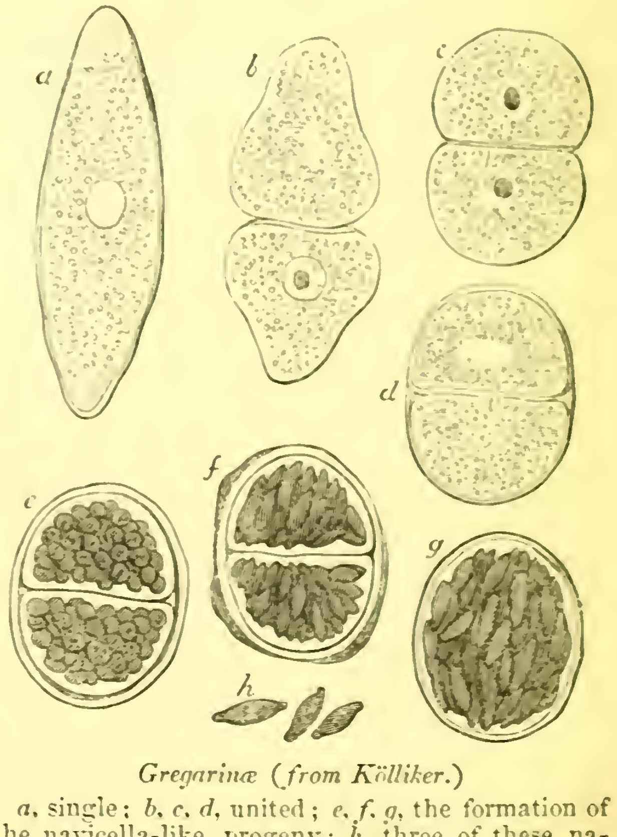
Formation and extrusion of ova or germs in Loxodes bursaria (from Cohn).

a, animalcule, containing two young; *b*, containing six; *c*, one of the embryos escaping; *d*, *e*, two ciliated embryos.

A similar production, but more numerous, of an internal progeny, has been observed in the microscopic parasitic animalcule termed Gregarina, which infests the intestinal canal of a number of insects, earth worms and some other invertebrate animals.*

The simple Gregarina consists of a single cell filled with granular substance, and containing a distinct nucleus. It has no intestinal canal, nor other internal organisation; is generally of an elongated shape, and creeps about by motions of slow contraction of its substance. The formation of the progeny or smaller bodies within the Gregarina is attended with a remarkable change in the parent animal, which has been carefully observed by Stein. This change, in which the animal appears double for a time, had been previously noticed by Kölliker and others, and had been interpreted by Kölliker as the conversion of a single animal into two, by a process analo-

Fig. 5.



Gregarinæ (from Kölliker.)

a, single; *b*, *c*, *d*, united; *e*, *f*, *g*, the formation of the navicella-like progeny; *h*, three of these navicellæ (from Stein).

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ferred to under the head of 'sporiferous reproduction,' by Prof. Rymer Jones, in the article POLYGASTRIA.

* Stein, Untersuch. üb. die Entwick. der Infusorien, Wiegmann's Archiv., 1849, vol. 1. p. 134. in Actinophrys, Acineta, and Chilodon uncinatus. Cohn, in Zeitsch. für Wissensch. Zoologie, Nov. 1851, p. 257.

* These animals were first accurately described by Leon Dufour in 1837 (Ann. des Sc. Nat. vol. vii. p. 10.). They have since been studied with great

gous to transverse fission. Stein, on the other hand, has been convinced by a very attentive observation of the different stages of this process, that it is of an opposite character, and that, previous to the development of the young progeny, two of the Gregarinæ have become fused, or united into one. As the two are about to unite, they gradually change their form from that of elongated planaria-like animalcules, to that nearly of hemispheres, closely pressed together; then a complete fusion or union occurs, and the whole of the granules of both having become amalgamated in one sphere, the development of the internal progeny takes place gradually from the mass. This progeny consists in a vast multitude of minute bodies, shaped like the Navicellæ (among the Diatomaceæ), but different from these bodies, and very probably constituting the reproductive germs or embryos of Gregarinæ. The development of this Navicella-like progeny into the Gregarina does not appear as yet to have been traced; as in this animal, like many other parasites, the progeny is required to migrate during its development from one stage to another, and the little bodies are passed out of the alimentary canal of the insect before undergoing farther changes.

The views and observations of Stein, however, should they be confirmed by others, would prove the very remarkable fact, that the phenomenon of conjugation, or fusion of two unicellular individuals, hitherto supposed to be confined to some of the simpler plants, as Closterium, Spirogyra and Zygnema, &c., may occur also in animals of a similar simple structure.

These observations on the Gregarina are not altogether of an isolated kind. In a recent interesting notice of this subject by V. Siebold*, he has called attention to the observation of Kölliker on the conjugation or fusion of two individuals of Actinophrys†, a spherical infusorian animalcule analogous to the Amœba or Rhizopoda, by its slowly contractile, amorphous texture, and its long, radiating, contractile processes. Kölliker observed two individuals of this animalcule to approach each other, adhere, and gradually to fuse into one, which soon assumed the same globular form, with the radiated contractile processes, as each of the two that formed it, and differing only from them by the increase of size which it sustained. This very curious observation has been confirmed by Stein, in an allied genus Podophyra, both of the sessile and pediculated kind; and V. Siebold has observed the same phenomenon in a species of Acineta belonging to the same family of Infusoria. Cohn, also, has repeated and confirmed Kölliker's observations in the Actinophrys sol, and has made a farther discovery of great interest in connection with the process of conjugation in these animals, having observed after the union, both in the Acineta and Actinophrys, the development, at certain periods, between the united individuals, of a spherical body of considerable size, vesicular form, and containing within it a nuclear formation of variable magnitude.

Although the farther development of this body has not yet been traced, it seems not improbable to V. Siebold that it may be analogous to the reproductive capsule or sporo-cyst of the conjugating Closterium or Zygnema*, from which bodies it seems to be certain that a number of reproductive spores are produced.

Since the foregoing was written, indeed, renewed researches by Stein† have come under my notice which are confirmatory of the view previously stated as to the reproductive process in Gregarina, and explain in a great degree the apparently incomplete observations of Pineau‡ and others as to the varying conditions of Vorticella, and also extend our knowledge of the production of germs of the Infusoria. Stein observed the Vorticella microstoma to lose its pedicle, become free, assume the globular form, and at last to be enclosed in a cyst produced by exudation from its own body. After a time the band-like nucleus of the encysted Vorticella is divided into a number of small discoid bodies, not by a regular or progressive process of cell-cleavage, but at once and directly. These minute bodies gradually increase in size at the expense of the granular and fluid substance surrounding them in the cyst, and ultimately escape in the form exactly of Monas colpoda (of Ehrenberg). These very soon fix themselves; and a fine pedicle is developed at the place of attachment. In other instances the Vorticella-cyst was observed to send forth long contractile processes from its surface, and then assumed very much the form and appearance of an Acineta or Actinophrys; and in this case a new Vorticella was formed in the interior in the manner of a bud. The Vorticella, therefore, it would appear, is capable of reproduction in two modes,—by the development of embryoes from the divided nucleus, which Stein on this account proposes to call nucleus germinativus (the testis of Ehrenberg); and by gemmation from an intermediate Acineta form. The first form Stein would regard as the equivalent of sex-

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success by various observers, as V. Siebold (Beitrag. Z. Naturgesch. Wirbellos. Thiere, 1839, p. 63.). Henle (Müller's Archiv, 1845, p. 369.), and Stein in the same, 1848, p. 182. Kölliker (Zeitsch. f. Wiss. Zool. 1848 and 1849), and as many as eighty different species of them have now been discovered.

[*] Zeitsch. f. Wissensch. Zool. March, 1851, p. 62.

[†] Op. cit. 1849, p. 207. In this very interesting memoir Kölliker has proved the animal nature of the Actinophrys by his observations on its contractility, and on the manner in which the particles of solid matters, vegetable and animal, are involved in its substance for the purpose of digestion, and their remains again rejected when that process is completed.

[*] See the Article Vegetable Ovum for an account of this process in the lower forms of plants.

[†] Zeitsch. fur Wissensch. Zool. Feb. 1852.

[‡] Ann. des Scien. Nat. 1845 and 1848.

ual production; the second as coming under the category of alternate generation; and the Vorticella embryo of the Acineta-form either repeats its gemmal multiplication, or becomes encysted, and gives rise then by its nuclear division to embryonal production. Other new forms of Infusoria are described by Stein under the names Spirochona gemmipara, Dendrocometes paradoxus, and Lagenophrys vaginicola, ampulla, and nassa, in which the mode of reproduction is somewhat similar.

These observations at once show the importance of the views entertained by some authors as to the share the nucleus may take in new production, and strongly indicate that much still remains to be known from observation of the processes of reproduction among the Infusoria.

Should these observations be confirmed, another analogy, in addition to those already observed, will be shown to exist between the organisation and functions of the Protozoa, and those of the lowest plants.* The tendency of various other recent researches, to which it has been impossible to refer more particularly in this place, seems to be to show that, in addition to the more common and obvious mode of multiplication by division and gemmation, by which the Infusoria, when vigorous and well nourished, are reproduced, there are other means by which, in different circumstances, the more permanent reproduction of the species may be secured; that minute cells are formed within them for that purpose, which may at present be called reproductive cell-germs rather than ova, till a more complete knowledge shall have been obtained of their nature and of the circumstances attending their formation; and that it is very probable that in the protozoa, as in the simplest plants, the combination of the contents of two cells, to all appearance similar, may, as in the process of conjugation, be the necessary preliminary step to the development of the reproductive germs.

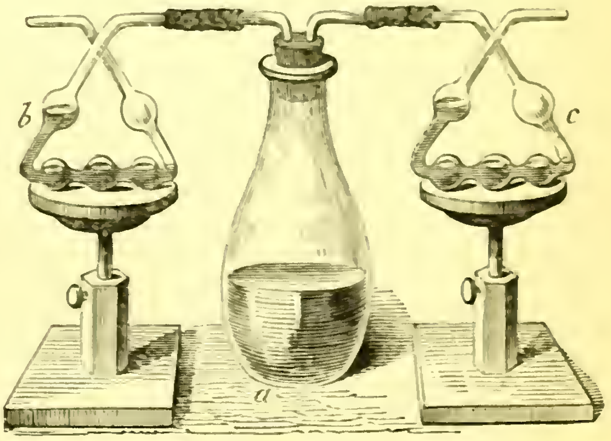
It ought at the same time to be kept in view that the Infusoria may, like many other animals, be subject, some to metamorphosis, and others to alternate generations. Already, since the publication of the great work of Ehrenberg, most important modifications of his system of these animals have been found necessary, and it seems almost certain that it is destined to undergo still farther changes, many of those forms which are now recognised as belonging to distinct genera and species being possibly no more than different stages of development of the same animal.

2nd. *Of the possibility of primary, direct, or non-parental production of animals, or of so-called spontaneous and equivocal generation.*

From what has before been stated as to the very general, and almost universal, existence of the sexual mode of generation among animals, and from the reasons that have been given for the belief that in those few and simple animals in which a sexual distinction has not yet been ascertained, there may still be propagation by means of minute germs, the reader will already have drawn a conclusion as to the very insufficient nature of the proof that can now be adduced in favour of the view that certain animals may arise independently of pre-existing individuals of the same species. The hypothesis might, perhaps, be at once dismissed with the remark of a recent writer*, "that it is safer to trust to generally prevailing laws, than to confide in such of our observations as are contrary to them." But as in the article GENERATION†, the author was led by a careful examination of the evidence then available on the subject, to admit the probability of the non-parental mode of production as an exceptional occurrence, at least among the lowest tribes of animals and plants, and as that hypothesis has since gradually lost more and more of its probability, from the accumulated opposing proofs resulting from more recent researches, so as, in his opinion, to be now no longer tenable, it may be proper at this place to review briefly the bearing of the present more advanced knowledge of the generative process upon this long and keenly debated question.

Admitting, in the meantime, that the ova, or separate germs of Infusoria, have not yet been discovered with certainty, there are not wanting direct experiments which demonstrate that in an infusion of organic matter which would, when exposed to the air, naturally furnish a rapid succession of these productions, the development of living organisms is entirely suspended, if the arrangements are made such as to render it impossible for any germ or other part of a previously existing infusorian animalcule or plant to be communicated to the infusion. The experiments of Schultze and of Schwann are valuable, as appearing to have secured, in a great measure, the above-mentioned conditions, without otherwise interfering with the validity of the result. The first of these ob-

Fig. 6.



Apparatus employed by Schultze to prevent the access of germs by the air to an infusion.

a, flask for infusion; *b*, tube, with caustic potash; *c*, tube, with sulphuric acid.

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* See the recent work of Alex. Braun, entitled Die Verjungung in der Natur, Freiburg, 1849.

* Eschricht, in Edinr. New Phil. Journ. vol. xxxi 1841. p. 355.

† P. 429.

servers* placed in a glass flask an infusion of organic matter, a portion of which was known from comparative trials, when left exposed to the open air, soon to have animalcules developed in it in great quantity, and he connected this vessel with a tubular apparatus, by two apertures, in such a manner that the air, which was made to pass frequently through the vessel containing the infusion, should be drawn through strong sulphuric acid, or potash solution, before reaching it; and Schwann† arranged a similar experiment, having in view to secure the like conditions, by causing the air, which had access to the infusion, to be previously passed through an iron tube at a red heat. Before the commencement of these experiments, the infusion and the apparatus were carefully subjected to the temperature of boiling-water, by which it was presumed the vitality of all ova, or germs, or other organic particles must have been destroyed: and the result was the same in both the series of experiments, — viz., that, after a considerable lapse of time, no animalcules nor confervoid plants were formed: but when the atmospheric air was afterwards allowed to pass freely over the same infusion, without being subjected to the processes before mentioned, a rapid production of infusory animalcules took place in the usual manner.

The results of these experiments appear to be on the whole satisfactory, and nearly to decide the question as far as relates to the probability of the introduction of the germs of Infusoria, &c., into infusions by the air. But, indeed, the failure of many experiments of this kind, when not performed with the most scrupulous accuracy, need not excite surprise, when the very indestructible nature of some kinds of infusory animalcules is considered. It has long been known, and has been ascertained by the careful experiments of Spallanzani, Bauer, and Doyère, that some of the Rotifera and Tardigrada are capable of supporting a high temperature without loss of life, and of being kept for years even in the state of complete dryness, without loss of vitality: and, although it must be admitted that these animals differ greatly in their organisation from the Polygastric Infusoria, and the latter appear to be very liable to destruction from slight causes, yet it is possible that their germs may resist destruction in a greater degree than their adult forms: and, should only one of these animalcules, or its germ, be left in any situation favourable to its development, it is easily understood, from what is known of the production of these beings, with what rapidity a vast multitude of them may be brought into existence by their ordinary process of fissiparous increase.

Most physiologists are inclined to reject as fanciful and inaccurate the alleged observations of the actual conversion of particles of organised or organic matter into living infusoria. At all events, statements of this kind are to be received with the greatest caution: such, for example, as the observations stated to have been made by Pineau*, who affirms that he has seen the direct conversion of particles of disintegrating muscular fibre, isinglass, and wheat-flour, into various forms of living infusoria.

The spermatic filaments also, which, so long as they were looked upon as independent animals, were referred to as examples of an undoubted spontaneous generation, furnish no evidence in favour of that hypothesis in the view in which they are now regarded by physiologists: for they are to be considered rather as a peculiar product of organic growth within the spermatic cells, somewhat analogous to the fine moving processes of the ciliated texture, than as distinct organisms.†

In so far, therefore, as the theory of spontaneous generation may have been supposed to derive support from the formation of the lower forms of plants and animals in infusions of organic matter, that hypothesis must be considered as having lost the greater share of its probability, if, indeed, it has not been entirely disproved: but it must at the same time be admitted that a more precise acquaintance with the nature of the germs from which these organisms take their origin is still required to render the arguments derived from this source entirely conclusive.‡

The external and internal parasites which infest the bodies of almost all animals have in former times been held to afford a still stronger presumption in favour of spontaneous generation than the production of infusoria; but it will be found that in this instance, to a much greater extent than in the other, the probability of the view has gradually passed away before the increasing knowledge which modern research has afforded of the various modes of propagation of these animals.

The ready communication of various Epizoa, or external parasites, from one animal to another is now well known, and accurate observations have demonstrated that in almost all instances this communication may be traced to the implantation of ova, or pregnant individuals into their parasitic abode, as in the researches on the Sarcoptes scabiei, &c.

The parasitic fungi, also, of various cutaneous diseases, as tinea, porrigo, plica polonica, foul ulcers, &c.; the yeast-plant, the vinegar-plant, and other minute fungi connected with fermentation; the contagious algæ of the batrachia and fishes; the muscardine of the silkworm, are all well proved to be communicable by the deposit of their spores, or some part of their substance, upon the external surfaces of the bodies of the animals on which they grow, or by their introduction into cavities opening on the exterior.

All the internal parasites, or Entozoa strictly so called, are now known to be capable of true sexual generation, by means of ova, in their perfect or complete condition, and the whole class is remarkable for the great development of the sexual organs, and the prodigious numbers of ova which they bring forth. But it has been ascertained that their ova are rarely developed into new beings in the place of the abode of the adult entozoa: they are commonly subject, therefore, to migration from one organ to another in the same individual, or from one animal to another, or from the parasitic to the free-living condition; and they have recently been discovered to present very remarkable changes of external form and internal organisation in their various habitations; so great, indeed, that many of them, previously believed to belong to species, and even to genera and families widely different, are now recognised as different conditions of the same animal or species, and that many forms, whose mode of generation was unknown, are found to be derived by indirect production from ova, in a manner which will be more particularly described under the next section.

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* Poggendorff's Annalen, 1837, and Edin. New Phil. Journ. vol. xxiii. p. 165.

† In paper on Fermentation, &c. in Poggendorff's Annalen, 1837, p. 184.

* Ann. d. Sc. Nat. March, 1845, p. 182.

† See Article SEMEN.

‡ Consult, especially, on the whole of this subject, Dujardin's Hist. Nat. des Infusoires, 1842.

Thus it appears that the only entozoa which are destitute of sexual organs, viz. those belonging to the division cystica, are very probably only imperfect forms of Taenia or other cestoids, which, so long as they are in the encysted or confined condition, do not reach their full development: but many of which, during their incomplete condition, are capable of being multiplied by a process analogous to gemmation.

The greater number of the entozoa breed only when in the alimentary canal of animals, and the ova are excreted along with the fœces: it is obvious, therefore, that very many ova must be destroyed, and that a few only are liable to gain those peculiar situations which are fitted to maintain them in their earlier conditions, or in their later stages, to bring them, as parasites, to their full state of development.

The entozoa are usually found, therefore, in their most advanced stage, in the alimentary canal. There seems, on the whole, little difficulty in accounting for the entrance of entozoa from without into the alimentary canal, or the pulmonary air-cells and other open cavities: and every new fact that has been observed relative to the occurrence of entozoa in man and animals, leads to the conclusion that the ova, or perhaps more frequently the earlier larval or undeveloped forms of the entozoa, gain access to these situations by introduction from without, and most frequently along with food and drink; in those instances at least in which the entozoa migrate from one animal to another, or from an animal to the free state before returning to the parasitic condition. But the entozoa, which are, in general, in an incomplete state when situated in the close cavities or solid textures of the organs of animals, sometimes make their way from these situations into the alimentary canal, there to undergo their final development. Such appears to be the case with the Strongylus armatus, living in an incomplete state in aneurismal sacs of the blood-vessels of the horse, and in a fully developed state in the intestine; the Strongylus vagans, in cysts of the porpoise, and afterwards free in the lungs; the Ligula or Bothriocephalus solidus, in cysts of the abdominal cavity of fishes, and afterwards in their perfect state in the alimentary canal of sea-birds. The Trichina and Echinorrhynchi, imbedded in the muscular flesh in great quantities, are no doubt imperfect forms of other worms, which must migrate from these situations to attain to their complete state.

With regard to the manner in which the entozoa inhabiting the close cavities of the body, or imbedded in the solid substance of organs, either in the free or encysted condition, gain access to these situations, which has to many appeared inexplicable, excepting on the hypothesis of their arising actually in the places which they inhabit, observations are no less decided in proving them to be of external introduction.

In the first place it may be stated that, although the ova of a considerable number of the entozoa are of so considerable a size as to render it improbable that they have passed as such through the capillary vessels, yet few, if any, of these larger kinds are observed encysted, and in others the ova are extremely minute, and might, without difficulty, be carried through most of the capillary vessels.

In the next place it may be mentioned that the embryoes, or earlier forms of various parasites, and the ova of others, have been observed in considerable numbers in the circulating blood of various animals *, as showing that by this means the entozoa may be carried in their small and early condition into any part of the body of an animal which is fitted to afford the conditions favourable to their farther development.

But in what manner have these bodies gained an entrance into the blood-vessels, or, in other instances, how may entozoa have penetrated into cavities or the parenchyma of organs, without being conveyed through the blood-vessels? To this question, also, recent observations seem to furnish a satisfactory answer: for it has been ascertained that, in a number of instances, smaller or larger entozoa, but especially the former, pierce the tissues of animals with great apparent facility, being frequently provided in the young state with an apparatus of sharp hooks for that special purpose. Some of them have been observed in the act of passing through the

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* I may here refer to the original observations of Schmitz, (Berlin. 1826), and the more recent ones of Valentin Gruby, Gluge, Vogt, and others. See Valentin, Repertorium for 1842 and 1843. The Annual Report in Müller's Archiv. for the same years, and in Wiegmann's Archiv. for Naturgesch. Valentin's account of the Ova of Distoma in the fluid covering the medulla oblongata of a fœtal sheep (Müller's Archiv. 1840, p. 317), and V. Siebold's Article 'Parasites' in R. Wagner's Handwörterbuch der Physiologie.

solid substance of organs or through membranes; and from the various stages of advancement of others already referred to, seen in different parts of the same animal, little doubt can prevail that they must have done the same: but the aperture through which they make their way, besides being in most instances very minute, seems to close very rapidly and completely after them. So that the occurrence of entozoa in entirely isolated cavities — such as the aqueous chamber of the eye, or in the parenchyma of solid organs, — does not now present to our minds any valid objection to the view that in all instances they are introduced from without; and it will be apparent, from the same considerations, that even the occurrence of entozoa in the fœtus, of which there are undoubted instances, and to which great importance has been attached as an argument in favour of their spontaneous origin, may be explained on the supposition of their ova, or young, passing from the maternal parent, through the blood-vessels of the umbilical cord, as is known to happen with various poisons.

The whole history, then, of this remarkable class of animals, as it is now known, tends to support the general conclusion that they are all capable in their complete state of sexual reproduction, and that they gain the various sites of their parasitic habitations by introduction of their ova, or embryoes, or of more advanced stages of their growth from without, either directly into the open cavities, or more indirectly, by piercing the coats of vessels, membranes, &c., into the close cavities and the parenchyma of solid organs.*

A candid review of the whole evidence on this question leads to the inevitable conclusion, that, though all the difficulties or doubts which surround it are by no means completely removed, the hypothesis of primary or spontaneous generation receives little or no direct support from the accurate observation of the mode of origin of those animals which alone were supposed to afford proofs of such a kind of production; and that this view must, therefore, on the strongest grounds of analogy, be in the meantime abandoned, for that which attributes the origin and reproduction of all organised beings to an undeviating connection through ova or germs, seeds or spores, between new individuals and others of identical species which have previously existed. And if the present somewhat imperfect state of knowledge does not permit us to affirm this absolutely, as the result of direct observation, the exceptions are so few and unimportant, that they may be disregarded in the overwhelming evidence of a positive character in favour of the opinion, derived from analogy, that every organic being, if not produced in actual union with another, derives its origin from a germ or some such connecting part that has proceeded from a being of the same kind.

If this be the present state of the argument in respect to the hypothesis of the first origin of organic beings, it need scarcely be added that the opinion which has attributed the production of various animals to conversion or gradual transmutation out of other species or genera, has still less of real to be adduced in its support. In the long series of ages in which authentic observations have been made on animals, no such examples have been ascertained, and there are no established facts which give any substantial grounds for believing that in the natural or wild state of animals there is any departure from that undeviating succession of specific resemblance between parent and offspring, which seems to form one of the most constant of the laws of organic nature with which we are acquainted.

3rd. *Production of dissimilar individuals among sexual animals by a non-sexual process: so-called Alternate Generations.*

From the foregoing general views it appears that in all Vertebrated Animals, and in by far the greater number of Invertebrated animals, the process of permanent reproduction consists in the development of the new being from the blastodermic mass formed by a peculiar process of cytogenesis in the fecundated ovum. But, as has already been shortly stated, there are some varieties among them in regard to the degree of directness with which the product of development from the ovum arrives at that state of maturity, or sexual completeness, in which it is capable of renewing the act of sexual generation. These varieties may be classed as follows:—1st. The product of the ovum, being single, attains by a gradual process of development, when it leaves the ovum at birth, to nearly the same form and structure as its parents: this is generally called *Embryological Development.* 2nd. The product of the ovum, being single, is born or leaves the egg at an early period, and while comparatively imperfect, or, as it is called, in a *larva* state, and by one or more successive changes of development of a marked kind, afterwards reaches the specific or typical form: these changes are usually called *Metamorphoses.* 3rd. The product of development from the ovum does not itself become a complete animal, but gives rise, by a peculiar mode of generation of a non-sexual character, and therefore different from that by which fecundated ova are formed, to a new body, or to successive progenies of new bodies, one or more of which ultimately attains to the specific resemblance of the sexual parents by which the ova were produced. This is the "Alternating Generation" of Steenstrup, or what we might with Mr. Owen, in contrast to Metamorphosis, call a process of *Metagenesis* *; and of which the single and multiple varieties might be distinguished according as the intermediate progeny consists of one or of successive new productions.

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* As to the bearing of a knowledge of the habits &c. of the Entozoa upon the question of their spontaneous origin, consult the able essay by Eschricht; "Inquiries concerning the Origin of Intestinal Worms &c." in Edin. New Phil. Journ. vol. xxxi. p. 314. 1841, the article on Parasites by V. Siebold, in R. Wagner's Handwört. der Physiol.; E. Blanchard's Researches on the Structure &c. of Intestinal Worms, in Ann. d. Sc. Nat. 1848 and 1849, particularly vol. vii. p. 121. Dujardin's systematic work, Hist. Nat. des Helminthes, 1845. And in connection with this and the whole subject of spontaneous generation, the Systematic Treatises on Physiology of Burdach, J. Müller, Valentin, and Longet.

In the two first and best known forms of sexual generation, the term Development has been usually given to a gradual process of changing and advancing growth by which the new animal is formed out of the ovum, till the period when it leaves it, or is said to be born; and the term Metamorphosis has been generally applied to certain more marked and sudden changes of growth, apparently depending on the circumstance of the embryo or young animal having left the ovum, or having been born, at an early period in a comparatively incomplete state of growth. But in establishing such a distinction between these terms, it is not meant to be affirmed that the changes which a young animal subject to metamorphosis undergoes are individually or on the whole greater than those which occur in an animal which attains to its full growth by a process of development; but merely that the one series of changes is less gradual than the other; and that the more marked changes which accompany metamorphoses are related to certain conditions necessary to enable the animal which is born at an early period immediately to perform those acts which belong to its independent existence. It would indeed not be difficult to show that the changes which a mammal or a bird undergoes during its viviparous or oviparous development, are quite as remarkable and complete as those which occur in the change of a Batrachian reptile from its aquatic to that of its air-breathing condition, or of an insect from its larva to its complete form.

In both of these instances one individual only is developed from the ovum, and that individual itself at last reaches sexual completeness, and as being well understood they need not be longer dwelt upon here. But in the varieties of the reproductive process which are now to be more particularly noticed, the individual that proceeds directly from the ovum does not itself pass through the whole series of changes which are necessary to bring it to the form of the fully developed animal; but before it possesses any sexual organs, or has attained to sexual maturity, it produces from a minute germ formed in its body by a non-sexual process, a new individual, or a succession of individuals, the last of which only attains to the specific resemblance of the parents, and acquiring sexual organs propagates the species by means of ova. This is the modification of the reproductive process already termed *Metagenesis*, and which has received so much attention under the name of "Alternate Generations" since the publication of Steenstrup's celebrated treatise under the title of "Generations-Wechsel" in 1842.*

No examples of this peculiar modification of the reproductive process have been known to occur in the Vertebrata, and with one exception they are confined to the lower and simpler of the classes of Invertebrated animals. They are not, however, entirely confined to the very lowest classes of these animals as distinguished by the Zoologist, but rather to the simpler and less developed members of each of the several classes in which instances of them have been hitherto observed.

The essential nature of this form of reproduction consists, then, in the development from the ovum of an individual which is dissimilar from the parent or parents producing the ovum, and in the succeeding production from that individual, by a non-sexual process, of a progeny of one or more, or a succession of individuals, of which the last of the series resumes the parental form. While in animals, therefore, reproduced by the ordinary form of generation, the species is composed of entirely similar individuals, or of individuals differing only in sex; in those animals which are subject to the alternate or intermediate generation, the species includes a variety of individuals usually of dissimilar form; of which some are without sex, and others are complete as regards the development of sexual organs.

It has appeared to some authors that the phenomena in question are to be regarded as no more than peculiar modifications of the processes of development or metamorphosis, of such a nature that the product of the ovum becomes multiple instead of, as is more usual, remaining in its single individuality. But to admit the correctness of this view, it would be necessary to employ these terms in a sense widely different from that commonly given to them; and, indeed, to modify the ideas of these processes of embryological development in a greater degree than seems warranted by what is at present known of their nature.

The name of *larva* is usually given to the imperfectly developed animal that is born or leaves the egg at a comparatively early period, and fitted for independent existence in that state; and in the changes of metamorphosis by which that larva attains to the complete specific form, great as these changes may in some instances be, we recognise that it is the individual produced from the ovum which itself undergoes these changes; whereas in the various kinds of alternate generation, it is always by the formation of an entirely new individual, arising from a minute germ connected with the first, but to be distinguished from its parts, and without a sexual process, that the species is at last completed. The new individual may be single or there may be a multitude of them; they may remain connected with the one producing them or they may be detached and live independently, but they nevertheless constitute different animals, and cannot be regarded in any other light than as so many individuals distinct from the one producing them, although all are descended from one ovum, or all are necessary to make up the entire species.

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* Adopting a term which has been used by Mr. Owen in his Lectures. Med. Times, vol. xx. 1849.

* A work which appeared originally in the Danish language, and in German in 1842, and of which an excellent translation into English has been published by the Ray Society in 1845.

And it is further to be observed that each of these several animals may be subject to individual metamorphosis, and that in some classes there is so gradual a transition from individual change to new production that it may be difficult to determine to which of these forms of reproductive development their phenomena ought to be referred.

In that part of the article which treats specially of development our attention may again be called to some of the more remarkable examples of individual metamorphosis that are known: at present it is intended rather to bring prominently forward those instances of alternate generation which have been discovered since the publication of the Article Generation, or which, if previously known, may now be viewed in a different light, in consequence of being brought into comparison with other observations of a similar kind and of more recent discovery.

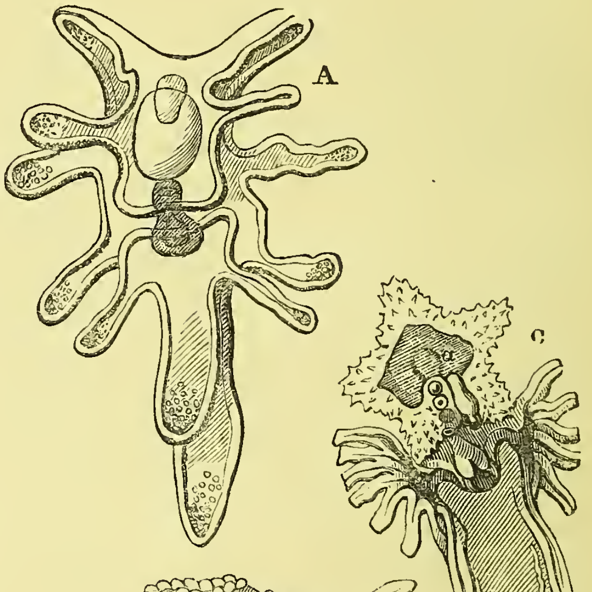
We may first consider some examples of this process, or of one very analogous to it, in which the new animal is single.

Echinodermata.— In several orders of this class a variety of the reproductive process has of late years been pointed out, in regard to which it may be doubted whether it is most of the nature of a metamorphosis or a metagenesis, but which, as it has been considered by J. Müller, the discoverer of the most interesting and remarkable of its phenomena, as in some measure analogous to the alternating generation, I will mention in this place; the more so, that it might almost be looked upon as forming the connecting link between the direct and the alternating processes of reproduction.

In some of the Echinodermata it appears from the earlier observations of Sars that the young produced from the ova are developed directly into the parental form, passing however through several marked modifications in the early stages of development. Thus, some of the star-fishes (*Asteracanthion glacialis*, Sars) leave the egg as a ciliated free moving animalcule, then they become pediculated and attach themselves, have four club-shaped processes developed on them, and, lastly, they pass by the development of the rays and the internal organs into the complete form; but here the whole, or nearly the whole, germinal mass of the ovum is converted into the embryo or larva, and the whole, or nearly the whole, of this undergoes the farther changes of conversion into the complete and sexual animal.*

From the researches of J. Müller it appears that the mode of development now described is exceptional among the Echinodermata, and that in other families of the erder Asteriadæ, and in the Ophiura and Echinidæ, an embryo or larva of a peculiar kind, is formed by direct development from the fecundated ovum, which is not itself converted into the complete animal, but rather serves as a temporary stock from which the perfect animal is subsequently formed in a manner that may be compared to gemmation. But it does not appear that more than one individual is developed from each primary larva stock, and this gradually dies away, so soon as its attached offspring has made some advance in its formation. This body, described under the name of Bipinnaria asterigera, as connected with an Asterias, is a comparatively large animal, with a long pediculated body, twelve or fourteen tentacles, an alimentary canal, consisting of mouth, gullet, stomach, in

Fig. 7.



Bipinnaria asterigera (from Müller).

A, the young larva before the Echinoderm is formed.

B, a more advanced larva, with the Asterias on its summit.

C, the Asterias torn up to show its stomach, a continuation of the alimentary canal of the larva.

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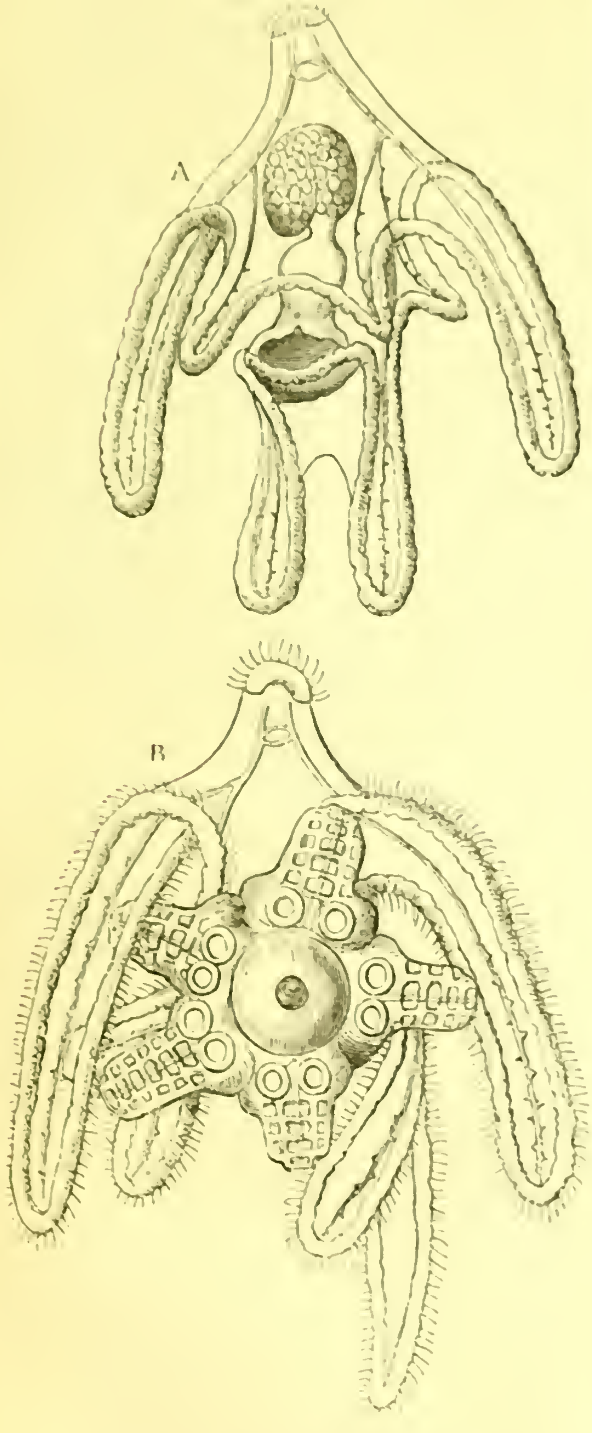
* Sars, Fauna Littor. Norvegiæ, 1846; and Ann. des Sciences Nat.; Agassiz, Lectures on Comparative Embryology, New York, 1849; and a Letter from Desor to J. Müller, in Archiv. für Physiol. 1849, p. 79.

testine, and anus, and moves actively through the water. Sars who had observed this body in 1835, was the first to suggest in 1844 that it might be the early condition of a star-fish [*], and this view was confirmed by the admirable researches of J. Müller [†], and by observations of Koren and Danielson [‡], who have shown that the Asterias is gradually formed out of a small granular mass which surrounds the stomach of the Bipinnaria, and becomes separated from the stock when in a comparatively early state of advancement. The larva stock moves about afterwards for a few days, and then appears to die without giving rise to any farther progeny.

Fig. 8.



Pluteus paradoxus (*from Müller*).

A, Pluteus before the commencement of the formation of the Ophiura.

B, Ophiura formed on the side of the gullet.

The gemmiparous larva of some other kinds of the Echinodermata was first described by J. Müller as a distinct animal, under the name of Pluteus, before he was acquainted with the phenomena of its subsequent development: in 1846 he traced the relation between one kind of this body which he had called Pluteus paradoxus, and the Ophiura, and between another kind of Pluteus and Echinus, ascertaining it to be the same that has just been stated to exist between the Bipinnaria and the Asterias. The Pluteus presents the form of a quadrangular pyramidal frame, with four large ciliated limbs at the angles, and four smaller ones suspended from the middle below, while the upper part is surmounted by a sort of dome. It bears some resemblance to a Beroë, and might be described as the ciliograde larva of an Echinoderm. The form differs, however, somewhat for various species of Ophiura and Echinus.

In the centre of the dome and round the mouth of the Pluteus a granular mass is described, and from the side of this, non-symmetrically, the gemmation of the new individual proceeds. The Pluteus moves at first with great activity through the water, propelled by its ciliated limbs and cirrhi; but as the new Ophiura or Echinus buds from it and spreads more and more over its dome, the Pluteus shrinks, becomes less active, and at last disappears.[*]

Various other forms of the Pluteus-like animal have been described by Müller, and the process of gemmation has been traced by which the new Echinoderm takes its rise within them. The result of these discoveries is already to throw an entirely new light on the nature and organisation of this class of animals; but the species of all of those observed is not yet determined, and something still remains to be learned of the exact mode of origin of the new animal. By some [†] the process has been looked upon merely as a secondary development from the remains of the yolk attached to the parts first formed; but the researches of Müller do not appear to give support to such a view; and would rather appear to show (as in Auricularia, *fig.* 9.), that the new animal is formed from a minute germ in a determinate part of the parent animal without that germ being traced to the yolk of the egg.

In a farther series of researches on the larvæ and metamorphoses of the Echinodermata [‡], J. Müller has pointed out that the Holothuridæ are formed from a larva body somewhat analogous to the Pluteus, but that, instead of a process of new formation, the whole of the larva is converted by a very remarkable metamorphosis into the Holothuria; and he has been enabled, from his own researches and the comparison of some others, to bring the whole of the Echinodermata under a general view, the result of which is the determination of the three following varieties of metamorphoses and production among them. In all of them the embryo, immediately developed from the ovum, has a bilateral symmetrical form, and passes by the subsequent metamorphosis into the radiated type. This change is, however, more or less direct, or by intermediate forms.

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[*] Wiegmann's Archiv. 1844. part i. p. 176.

[†] Mem. of the Berlin Acad. 1846 and 1848.

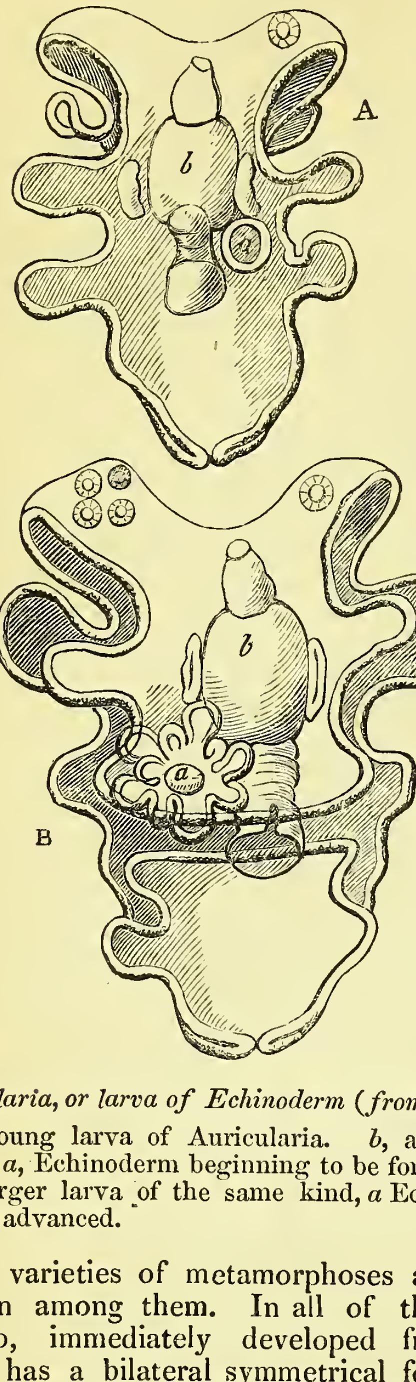
[‡] Ann. des Sc. Nat. 1847, p. 348.

[*] J. Müller, in Mem. of Berlin Acad. 1846 and 1848; Derbes, in Ann. des Sc. Nat. 1847.

[†] As Carpenter, loc. cit. p. 939.

[‡] Memoirs of the Acad. of Scien. of Berlin, Nov. 1849, and April 1850, published in 1851, p. 35.

Fig. 9.



Auricularia, or larva of Echinoderm (from Müller).

A, young larva of Auricularia. *b*, alimentary canal; *a*, Echinoderm beginning to be formed.

B, larger larva of the same kind, *a* Echinoderm farther advanced.

1. In the first variety the change of the bilateral larva, or embryo, into an Echinoderm takes place at its earliest period, when the embryo has a general covering of cilia, but not the special ciliated borders or limbs of the Pluteus. A part of the body of the embryo takes the form of the Echinoderm; the rest of it is absorbed into the body of the new animal. This occurs in a part of the Asteriadæ, as in Echinaster, Asteracanthion, and others, described by Sars, Agassiz, Desor, and Müller.

2. In the second variety the change occurs when the larva is fully organised, that is, when it possesses digestive organs and a special motor apparatus of ciliated borders or limbs. The Echinoderm is placed upon the Pluteus somewhat in the manner of a picture on an easel, or a piece of embroidery in its frame and stand, and incorporates a part of the digestive cavity with itself. The remains of the larva gradually disappear, as in Ophiura and Echinus; or are broken off and die, as in Bipinnaria.

3. In the third variety the change of the larva takes place twice. First, it passes from the bilateral type with ciliated borders into the radiate type, and having taken something of the shape of a barrel, it acquires a larval locomotive apparatus consisting of ciliated hoops; and then from this state the Echinoderm is developed without any part of the larva being separated. Either the Echinoderm is formed of a part of the Vermiform larva, and the rest of the larva is absorbed into the Echinoderm, as in Tornaria, or the whole larva is simultaneously transformed into the Echinoderm, as in Holothuria.

From Busch's observations it appears that the Comatula passes very rapidly through the stage of the bilateral form into that which Müller has called pupa with ciliated crowns. It is also an interesting fact in connection with the history of animal metamorphoses, that the early condition of the Comatula is that of a pedunculated Crinoid.

Müller has remarked that these phenomena partake in part of the nature of metamorphosis, and in part of that of the non-sexual gemmation of the alternate generations. As the Echinoderm arises like a bud in the larva, there is alternate generation; but as the essential internal organs (that is, the alimentary canal from the stomach to the anus, but not the mouth and gullet) are taken into the new animal, there is also true metamorphosis. "I understand," says he, "by alternate generations nothing more than the succession of two forms of organism, of which the one arises in or upon the other as a minimum, or as a bud; the second, that is, the developed bud, is destined for sexual generation, producing from its ova the non-sexual larva, which again is destined for gemmation."*

Adopting the view that the Echinodermata present an example of alternate generation, it is to be observed that the product is single in all the instances known: but in all the other forms of intermediate or alternate generation hereafter to be noticed, the product of non-sexual gemmation is multiple.

Polypina. — The animals usually comprehended in the general denomination of Polypes or Polypina present very various kinds of structure and degrees of complication in their organisation; and recent researches, as to their mode of development, which point out that some of them are subject to a process of alternate or dissimilar generation, would appear to indicate a very different distribution

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* Loc. cit. p. 106. The researches of J. Müller on this subject have been published in a separate form, as well as in the Mem. of the Berlin Acad. These Memoirs, and others on the same subject, will be found also in Müller's Archiv. 1846, p. 108; 1847, p. 160; 1848, p. 113; 1849, pp. 79. 84. 364. 400; and 1850, p 452.

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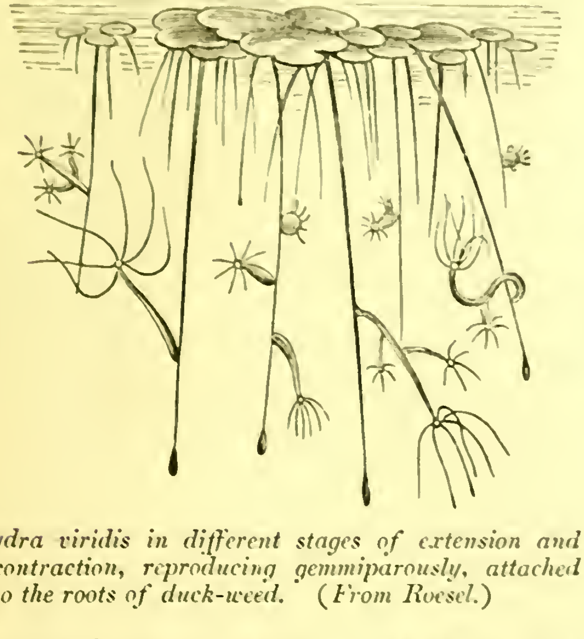
of these animals in the zoological system than that which has hitherto been followed. Most Naturalists are now disposed to separate from the true Polypina the Bryozoa, or so-called Ciliobrachiate Polypes, which, though presenting a considerable resemblance to the Polypes in their external anthoid appearance, yet approach much more nearly to the Tunicated Acephalous Mollusca by their internal organisation; and remarkable affinities have been pointed out between some of the Polypina and Acalephæ, which show that these classes, though very dissimilar in their external forms and mode of life, are in reality very closely allied in structure.

The greater number of the Polypina are aggregate or compound animals, that is, consist naturally of groups of individuals united or associated together on a common stem and branches, or on a more solid stock. But the common fresh water Polype, or Hydra, and the various Actiniæ of the sea coast, are, to a certain extent, exceptions to this general rule, and, as we shall see, differ also in regard to their mode of reproduction from most of the other families of this division of animals. The Actinia is usually a single animal: no doubt it is multiplied occasionally by buds, but these are thrown off and become developed usually in an isolated position. The Hydra sometimes occurs as a single animal, but more frequently during summer, and when well nourished, as a compound one; the multiple individuals being developed by gemmation from the first or principal stock, and also themselves forming younger progenies by budding; but the individuals so formed on the Hydra generally separate from the parent stock when they have attained to maturity, migrate, and establish themselves as independent animals, to form new buds.

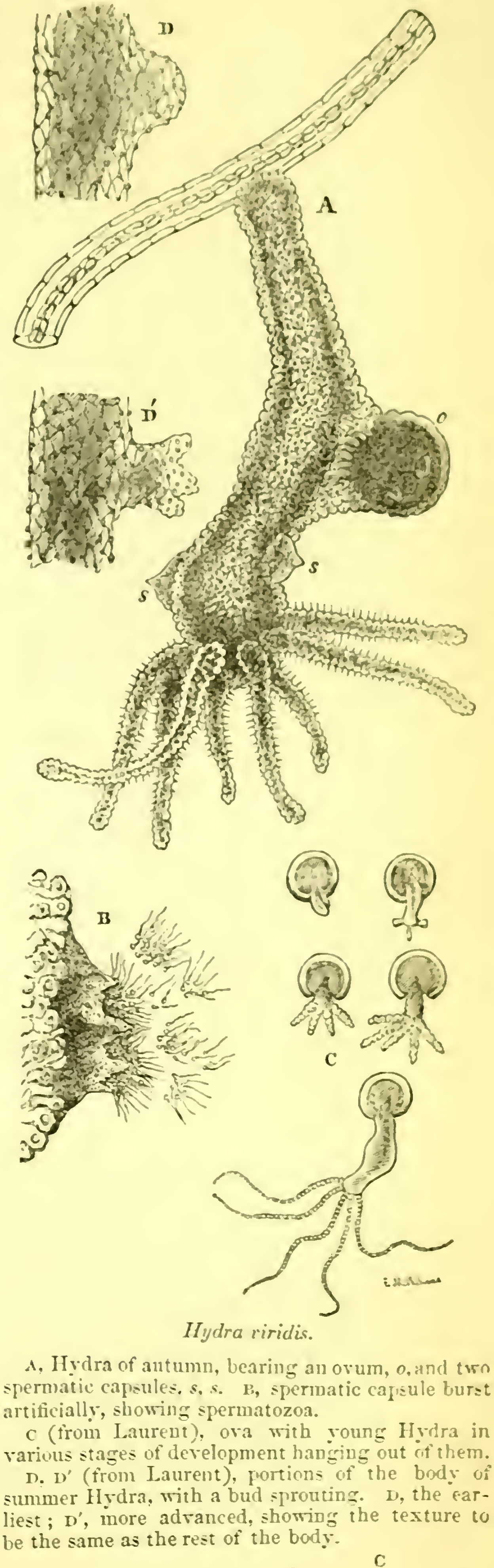
Fig. 10.



Hydra viridis in different stages of extension and contraction, reproducing gemmiparously, attached to the roots of duck-weed. (*From Roesel.*)

Both of these animals are capable of propagation by ova formed in the sexual way: in Actinia this seems to be the more common mode of its multiplication, the ova being fecundated and developed within the body of the hermaphrodite parent; but in Hydra it would appear that it is principally in the autumn, on the approach of cold weather, that the sexual mode of propagation is substituted

Fig. 11.



Hydra viridis.

A, Hydra of autumn, bearing an ovum, *o*, and two spermatic capsules, *s*, *s*. B, spermatic capsule burst artificially, showing spermatozoa.

C (from Laurent), ova with young Hydra in various stages of development hanging out of them.

D, D′ (from Laurent), portions of the body of summer Hydra, with a bud sprouting. D, the earliest; D′, more advanced, showing the texture to be the same as the rest of the body.

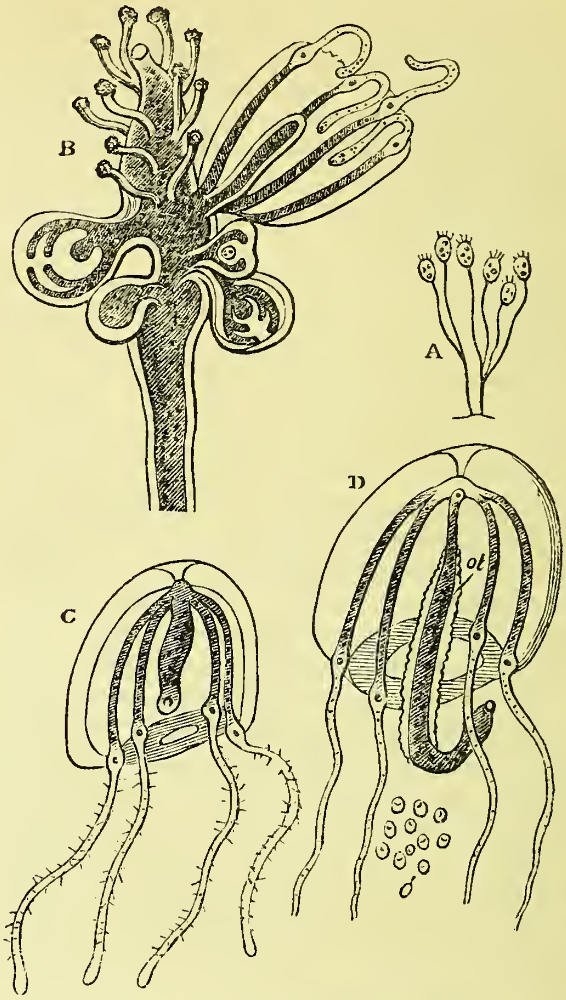
for that of gemmation which takes place throughout the whole of the summer.*

The ova of Hydra are simple vesicular capsules of a brownish colour formed in the substance of the wall of the animal's body, and separated from it previous to the development of the young; while the spermatic filaments are formed in smaller conical capsules placed nearer to the base of the tentacula either in the same or in different individuals.† The formation of the young Polype has been observed by Laurent ‡ to take place directly from the internal substance of the ovum, in which, however, he has not traced in a sufficiently complete manner the individual steps of the changes of development (*see fig.* 11. C.). The origin of the ovum in this animal is shown to be quite different from that of a bud: the former having the shape of a distinct vesicle from an early period, the latter not being perceptibly more than an extension of some part of the substance of the wall of the body, and precisely of the same colour and structure (*see fig.* 11. D, D′.).

The Hydra, therefore, while propagating very frequently by gemmation, is capable of reproduction also by fecundated ova, which are directly developed into the parental form. But many of the true Compound Polypes present examples, in their multiplication by gemmation, of the production of intermediate forms of animals between the ova and the perfect sexual individual, — a mode of reproduction, therefore, which may be referred to Steenstrup's general law of Alternate Generations.

Thus, to begin with the simplest form of these animals bearing the nearest resemblance to the Hydra, in the Coryne and Syncoryne, at certain seasons of the year, multiplication takes place from the stem or root by gemmation, the buds being developed in the form of attached Polypes; but at other times there are developed from the buds, without the concurrence of sexual organs, a set of delicate Medusa-like animals, similar to the Oceania, or those of the naked-eyed kind: these soon become detached, swim about freely in the water, acquire some of them male and others female sexual organs, and produce fecundated ova. These ova give rise, by their development, to a ciliated moving embryo: this soon becomes fixed to a spot, and is gradually converted into a Polype, similar to that from which the Medusa-like animals were formed.*

Fig. 12.



Syncoryne, developing a Medusoid progeny. Oceania (*From Désor.*)

A, natural size.

B, a portion enlarged, showing the budding of Medusoids in different stages.

C, one of the Medusoids, naturally detached.

D, another, farther advanced; *o t*, ovary, or testicle, placed on the alimentary canal; *ó*, ova.

R. Wagner appears to have been the first to observe Medusoid bodies produced from the Polype animals, as in Coryne aculeata, in 1833†, but the more full observation of the remarkable phenomenon of their formation is due to the researches of Sars, Löwen, Steenstrup, and Van Beneden, who have ascertained the relations of the Polype larva and Medusoid progeny, and the production of ova from the latter. Dujardin ‡ has also carefully traced the production of the free Medusoid bodies from a Syncoryne, which he has called Stauridia, and has farther ascertained the sexual condition of these Medusoids, observed the formation of their ova, and the subsequent development of these ova into Polypes.

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* This effect of the cold season in changing the mode of production from gemmation to oviparous formation, thus checking growth, but providing for the preservation of the species through the winter, is, as remarked by Dr. Carpenter, an interesting analogy with the change that is known to occur in the mode of production of the Aphis insect; see Principles of Physiology.

† The co-existence of ovigerous and spermigerous capsules on the body of the Hydra has been observed by many, as, first by B. de Jussieu, in 1743; (Abhand. der Swed. Acad. 1746, vol. viii. p. 211): by Trembley, in 1744 (Mém. sur les Polypes d'Eau douce); by Rösel (Insecten-Belustigung); Pallas, in 1776 (Karakteristik der Thier-pflanzen, p. 53); and more recently by Ehrenberg, in 1836 and 1838 (Verhand. der Naturforsch. Freunde in Berlin, 1838, p. 14); V. Siebold (Lehrbuch der Vergleich. Anat.); and by myself (Edin. New Phil. Journ. 1847).

‡ Nouv. Rech. sur les Hydres d'Eau douce, 1844, Voyage de la Bonite.

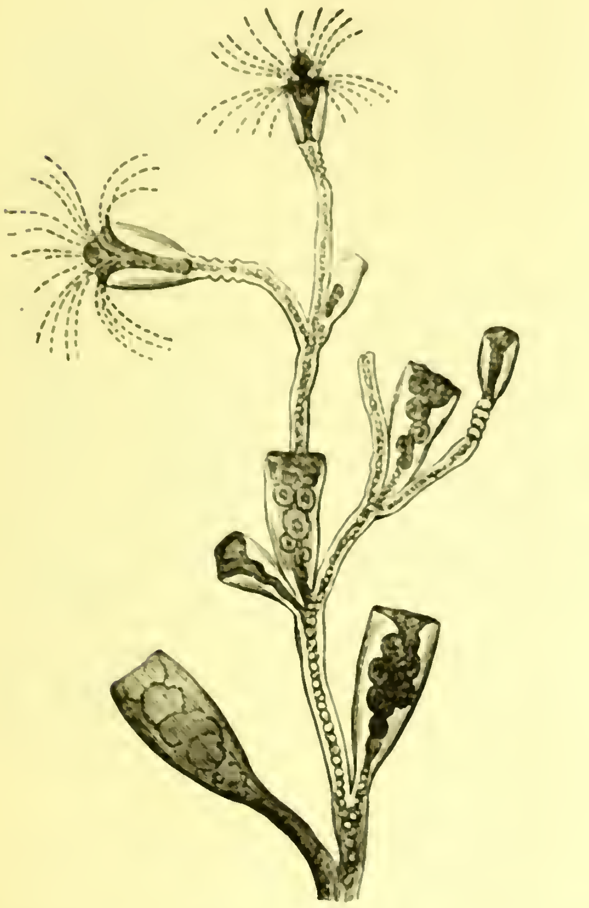
* See fig. of Syncoryna Sarsii, from Sars, Fauna Litt. Norveg. 1846; and Steenstrup's figures of Coryne fritillaria, tab. 1. figs. 41. 43, and Desor, in Ann. des Sc. Nat. 1840, pl. 2. figs. 13. to 16.

† Isis for 1833, p. 256. Also in Coryne vulgaris, in Icones Zootom. Tab. xxi. 1841.

‡ Annal. des Sc. Nat. 1845.

In a certain number of the Campanulariæ, Sertulariæ, and Tubulariæ, of which the internal structure is more complex than in the Coryne, and in which the Polype always naturally presents a branched form, or groups of distinct Polype heads formed upon a common stem by gemmation, it is now well ascertained that the Polype state is not the only nor the complete condition of the animal, but that by a process, in some instances similar to that above described, in others, somewhat different from it, a set of bodies, charged with the office of the sexual production of the ova, are developed in place of the more ordinary Polype heads or individuals. In the Campanularia gelatinosa, according to Van Beneden, the generative heads are close bell-shaped capsules, within which small Medusoid bodies are developed by a process apparently analogous to gemmation, or, at all events, without sexual generation, and each of these Medusoids becoming free, move about in the adjacent fluid as independent animals. The farther destination or changes of these Medusoid bodies have not yet been observed, but from parallel observations in other similar animals, it is believed that they afterwards attain to sexual completeness, and form ova which are developed into the Polype form.*

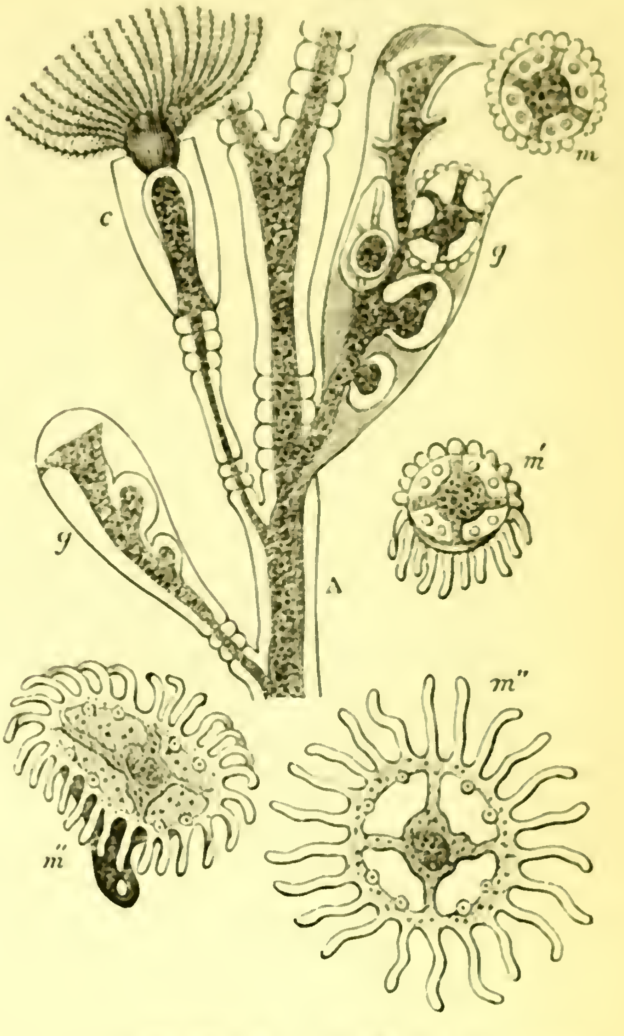
Fig. 13



Branch of Sertularia geniculata, magnified, shewing polypes, and ovigerous capsules.

But the interesting observations of Lovèn*, and also some previous observations of Lister†, would show that in the Campanularia geniculata, and in Tubularia, the Medusa-like bodies may in some instances not be detached from the Polype heads or capsules, and may even not be developed fully into the Medusa form, but nevertheless produce their ova in that attached situation, and thus give rise to ciliated embryoes, which, when excluded, move for a time, and then, like the others arising from the detached Medusæ, become converted into Polypes.

Fig. 14.



Campanularia. (From Désor.)

A, portion of a branched stem, magnified. *c*, non-sexual head or individual; *g g*, two capsules, or modified heads, producing Medusoids by gemmation, in different stages; *m*, Medusoid escaping; *m' m''*, Medusoids more advanced, moving freely by the contractions of their disc.

According to Désor, of Boston‡, the same Campanularia may at one time produce two kinds of capsules, the one set containing ova the other spermatozoa; the Medusoid progeny not being developed, and the ova giving rise to forms similar to the parent Polype: and M. S. Schultze, of Greifswald, has confirmed this statement§, apparently without the knowledge of Désor's observations, and has farther proved the necessity of fecundation for the development of the ova so produced in the Campanularia geniculata (*see fig.* 15. C.).

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* See the View of Campanularia geniculata, by Van Beneden, in Mém. de l'Acad. de Bruxelles, 1844, vol. xvii.; and Ann. des Sc. Nat. tom. xx. p. 350, 1843. See also the very interesting account of Tubularia, in Dalyell's Remarkable Animals of Scotland.

* In Wiegmann's Archiv, 1837.

† Phil. Trans. 1834.

‡ Ann. des Sc. Nat. 1849. xii. p. 208.

§ Müller's Archiv, 1850. p. 53.

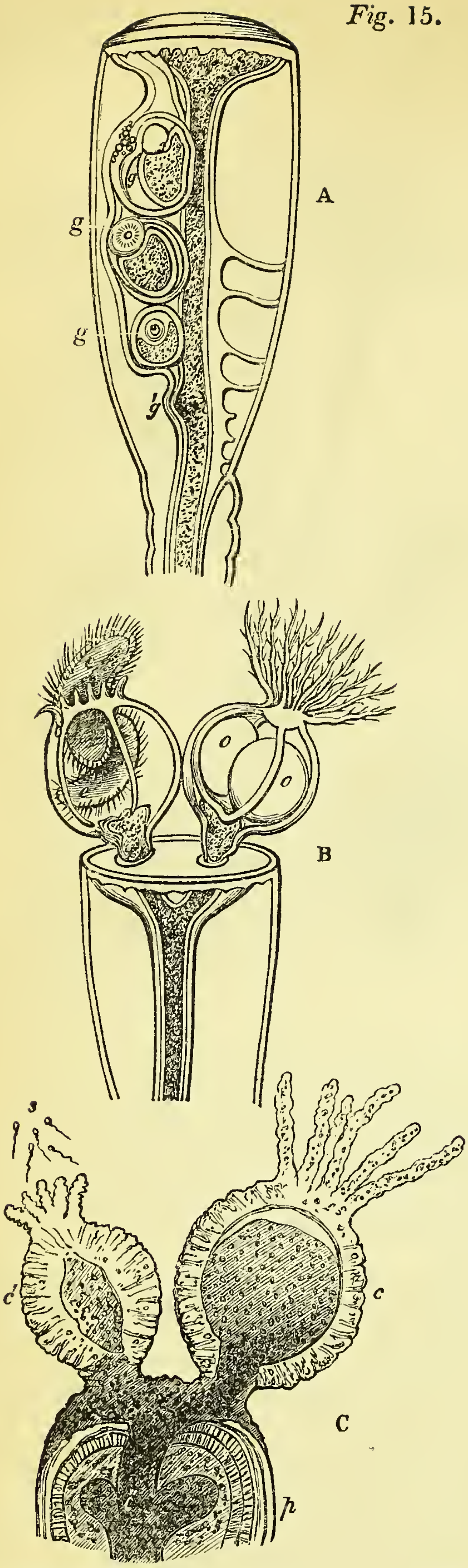
The various modes of production as they have been observed in the Tubularia by Van Beneden*, have been so fully detailed in the Article Polypifera, that the reader is referred to that article for an account of them. But it is to be observed that the reconversion of the Medusoid progeny of this animal into the Polype form described by that author (see Article Polypifera, *fig.* 50., p. 45.), has not received confirmation from the researches of other naturalists.

Much remains still to be learned of this remarkable process; but enough has been ascertained to show that in a certain number of animals, usually known as passing the greater part of their lives in the Compound Polype condition, the state of sexual completeness frequently belongs not to the Polype, but to a progeny having the form of a Medusa, and produced by a non-sexual process of development from the Polype stem.

Acalephæ. — Some time before the peculiar history of the development of the Polypina, now sketched, was discovered, an equally curious and unexpected phasis in the generation of some Acalephæ or Medusæ had been established by the concurrent researches of several inquirers; by which it was shown that the animals familiarly known as sea nettles existed for a time in the early stages of their development in the form of an attached polypoid, and were produced by a process analogous to gemmation, or transverse fission, in numbers from this Polype stock.†

Adult Medusæ are perfect animals in which the male and female sexual organs are placed on distinct individuals. The fecundated ova which they produce are first developed into a ciliated moving animalcule somewhat like a polygastric infusorian. This creature, after

Fig. 15.



Campanularia geniculata (A and B *from Lovèn, as copied by Steenstrup*).

A, modified or bell-shaped polype head or capsule, producing the female individuals at *g,g,g*; the earliest of these budding from the granular stem *g'*.

B, the female heads expanded from the bell: one of them containing two ova, *o o*; the other containing two ciliated embryoes, of which one is issuing at the summit of the attached medusoid, *e e*.

C (*from Schultze*), male heads of the same species of Campanularia; *p*, upper part of the polype head, or bell-shaped capsule; *c*, sexual capsule, or modified attached Medusoid, containing spermatozoa; *c'*, another of the same, burst, and spermatozoa discharged, *s*; *c''*, other spermatic capsules advancing behind the first.

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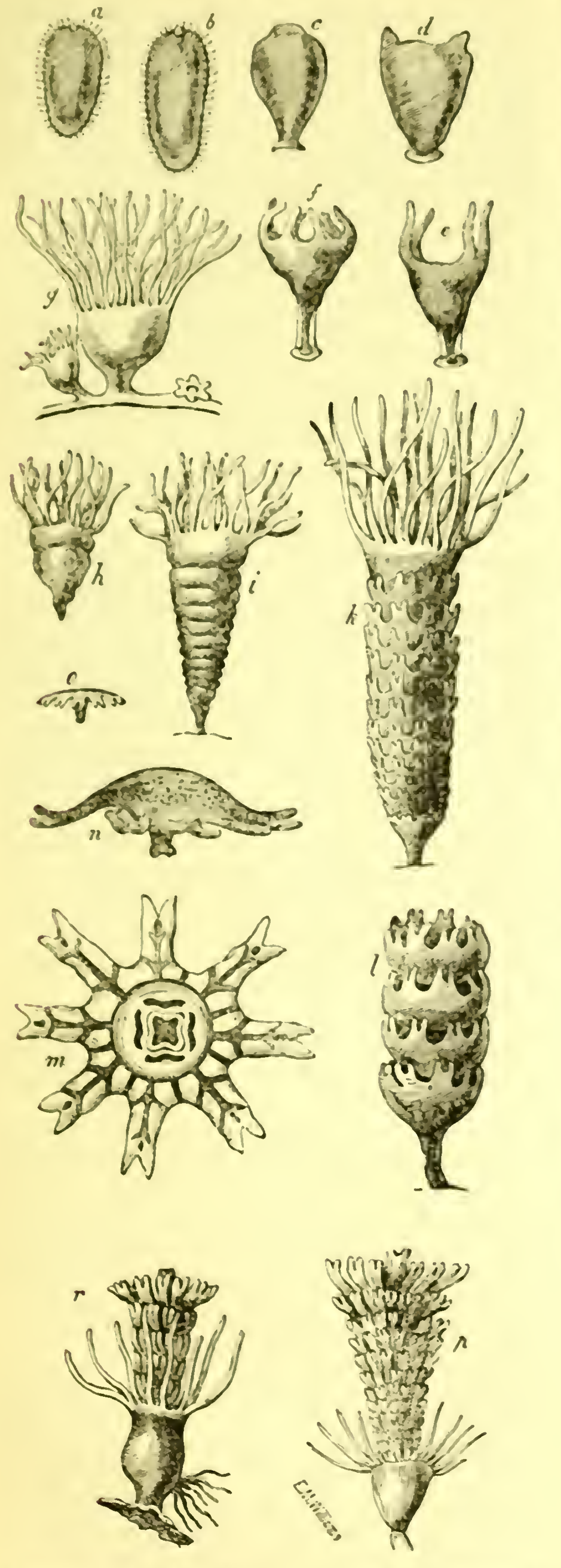
* Mém. de l'Acad. de Bruxelles, tom. xvii.

† The Swedish naturalist Sars appears to have taken the lead in this discovery, as early as 1828, by his observation of the Compound Polypoid, from which the Medusæ are thrown off; and subsequently, in 1835, by the discovery that this animal, or strobila, is really the young condition of a Medusa, or rather a colony of Medusæ. Very interesting observations of a similar kind were published by Dalzell on this body, under the name of Hydra tuba, in 1836, but his observations probably date from an earlier period (Edin. New Phil. Journ. vol. xxi. 1836). Sars pursued the investigation of the process further, and published the results in Wiegmann's Archiv, 1837; but the complete account of his observations was not published in the same Journal till 1841; see also Ann. des Sc. Nat. for 1841. In the meantime V. Siebold had arrived at precisely similar conclusions, and subsequently their views have been fully confirmed by Dalyell (Remarkable Animals of Scotland); J. Reid (Ann. of Nat. Hist. 1848, and Physiolog. Researches); Steenstrup (Alternations of Generation); and Huxley (Phil. Trans. 1849, part ii.) See also Dujardin, Mém. sur le Développement des Méduses et des Polypes Hydraires, Ann. des Sc. Nat. 1845. The reader is also referred to Dana's great work on Zoophytes in the United States Exploring Expedition. Philad. 1848.

undergoing a slight change of form, fixes itself by the narrowest end, and acquires tentacles like a Polype at the other, amounting for some time to eight. In this condition it appears to be capable of multiplying itself, or producing other similar attached Polypes by gemmation from its side or base, or from a running stolon below it. The subsequent change of each of these polypoids is remarkable. It has been described by Sars and Dalyell as follows: — The body undergoing some elongation becomes partially divided by transverse grooves, into a range or column of imperfect Medusæ, attached still to each other by their adjacent surfaces, but presenting at their borders, in various degrees of advancement, the division into rays or lobes which belong to the Medusa; the upper or terminal one having developed upon it a set of radiated processes distinct from the tentacles of the Polype and much longer than those of the rest. These young Medusæ are successively separated from the stock by the deepening of the transverse clefts between them. They then move about as independent animals, and proceed in their farther growth and development to sexual and other completeness. These bodies, therefore, are subject to two kinds of multiplication, which are very different: by simple gemmation a number or a colony of Strobilæ may be produced, and by transverse fission and development a number of Medusæ may be thrown off from each Strobila.

Fig. 16.

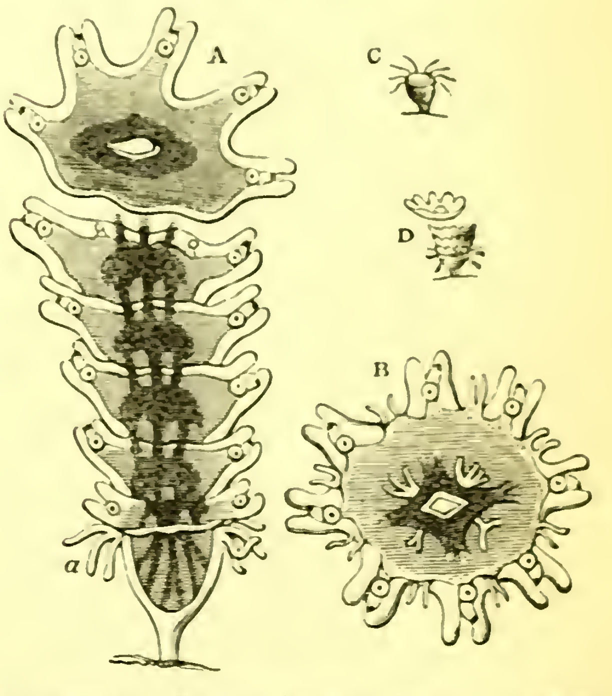


Development of Medusæ. (From Sars, Steenstrup, and Dalyell.)

a, b, ciliated free moving embryo from the ovum; *c*, embryo attached by its pedicle; *d*, its tentacula beginning to be formed; *e*, with four, *f*, with eight tentacula; *g*, the fully developed polype, producing other polypes by gemmation; *h, i, k*, transverse division and development of Medusæ from the polype stock or strobila; *l*, a pile consisting of four Medusoids just about to separate; *m, n*, and lower lateral view of Medusæ separated from the polype stock; *o*, more advanced, natural size: *p, r*, (*from Dalyell*), *p*, a pile of medusa discs separating, and new tentacula formed on the polype at the base; *r*, the same, with more of the discs separated; the strobila returning to its polype state and budding at the side.

A considerable number of the Medusa progeny having been separated, the Strobila stock generally returns to its polypoid condition,

Fig. 17.



Production of Medusæ (Aurelia aurita) from Polype stock. (From Désor.)

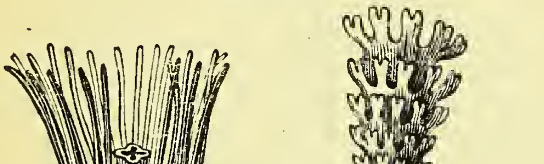
A, Medusa-form larvæ on the stock above the polype, which remains at the base, *a*.

B, lower surface of a detached Medusa.

C, D, natural size. Young Medusæ forming from the polype above its disc.

and may remain for a long time in that state; continuing to multiply by budding into others of the same kind, and occasionally giving rise by the process of fission to its Medusa progeny. The observations of J. Reid * have shown that the Polype or polypoid stock may remain for a very long time in this condition without forming any Medusa progeny; and these observations, as well as those of Steenstrup and of Désor, appear to show that these Polypes bear a considerable resemblance in their internal structure to the Medusæ which they produce by gemmation. The latter author, indeed, is inclined to believe that the new Medusa animals are produced not by a mere transverse fission of the Polype, but by successive gemmation on its summit, that is, round its mouth and within the tentacula; and he states that he has observed the Polype remaining with its tentacles at the base of the Strobila of Medusæ. The observations of Dalzell and J. Reid appear, however, inconsistent with this view; but it is possible that there may be varieties in respect to the mode of formation of the Medusa progeny, so that in one set the tentacles of the Polype may be included in the upper Medusa, and when all the progeny is separated, new tentacles may be formed on the Polype stock at the base, while in others the budding Medusa may be within the circle of the tentacula of the Polype.

Fig. 18.



Medusa larva. (*From J. Reid.*)

A, Polype before it has undergone any gemmation of Medusæ, showing the mouth and four canal openings.

B, the strobila or larva forming Medusæ.

C, lower surface of one of the young Medusæ, after separation.

It appears from recent investigations that others of the Acalephæ also undergo remarkable processes of non-sexual multiplication. According to Huxley's recent most interesting researches *, the Physsophoridæ, Diphydæ, and Physalia, are to be regarded as compound organisms in which the floating processes of most various form are analogous to Polype or attached Medusa individuals, which are the bearers of sexual organs, in some of one kind, in others of both, and others of which are neuter, on the same compound stock.† These are probably a progeny developed by budding from a single individual, which is the parent stem.

By these discoveries a remarkable relation is shown to exist between the medusoid and polypoid animals. Some we have been accustomed to see principally in their largest and most developed condition as Medusæ, others are best known in that polypoid condition in which they remain for the longest time; but we must regard that condition in which sexual reproduction takes place as the complete one, and this we have seen is in both the Acaleph or Medusa form, while the Polype or polypoid state, however permanent it may appear, is to be looked upon as a preparatory stage, in which, it is true, multiplication of its own kind may occur by gemmation, but which can only effect the true reproduction of the species by forming its progene of Medusans to which is committed the offic of producing the fecundated ova. This, therefore, is another example of multiple metagenesis, or alternating generation.‡

Mollusca. — Among the Mollusca the only examples of alternate generation that are yet known have been observed in the Tunicated Acephala: and among these, three modifications of the reproductive process are known in the Bryozoa, Ascidia, and Salpidæ.

The Bryozoa, or so-called Ciliobrachiate Polypes, long ranked with the Polypes on account of their union in branched groups, their radiated arms, and retractile body, but now regarded as more nearly allied by their internal organisation to the Tunicated Mollusca, present a very marked example of the multiplication by budding of the progeny of a single ovum. These animals never continue for any considerable time as single or distinct individuals, but, multiplying by gemmation, form numerous colonies, in which the new individuals remain connected with the primitive one from which they have proceeded and with each other. They thus always constitute compound groups spreading from the first individual as from a centre. All the individuals of the group may acquire sexual completeness, and the male and female organs are united in each individual: the ova are fecundated within the cavity of the mantle;

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* Ann. and Mag. of Nat. Hist. 1848.

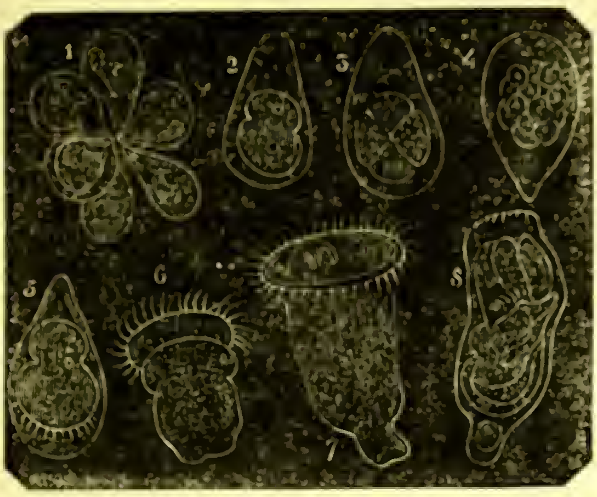
* Phil. Trans. 1849, Pt. ii.

† Professor Goodsir has informed me that his observations on Stephanomaia are quite confirmatory of this view.

‡ See also on this subject the interesting treatise by Prof. E. Forbes, on the Naked-eyed Medusæ, in Ray Soc. Pub. 1848.

on leaving the parent body they become developed into a ciliated embryo, which, for a time, moves freely about, then becomes fixed, undergoes farther changes in being developed,

Fig. 19.



A series illustrating the development by ova of Pedicellaria. (*After Van Beneden.*)

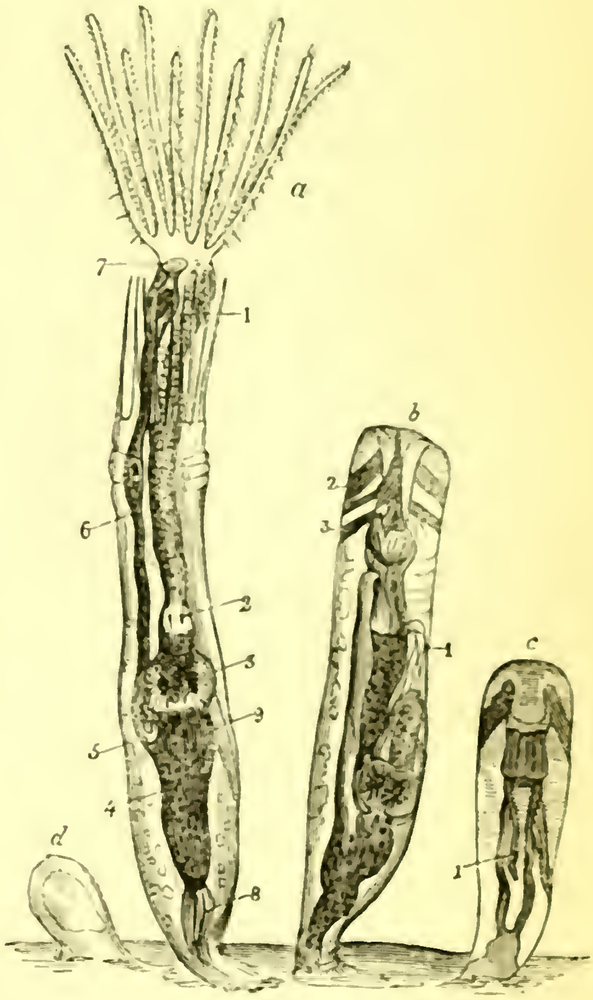
and now from its own body in some, and in others only from the spreading part of the stem or base which supports it, proceeds the gemmation of other individuals of the colony, all of which apparently are capable of sexual generation when they arrive at maturity.‡

The Ascidian Tunicata present another modification of the reproductive process now under consideration. Two forms of these animals exist, both perfect, viz. the simple and the compound; but these are not related to each other in the same manner as the two kinds of Salpians; for each kind is capable of propagating its like by generation. The solitary ones rarely multiply by gemmation, and when they do so the individuals separate from the stock; but the compound animals always undergo this mode of multiplication, and the multitude of individual Ascidians are in this form collected together in a mass of various shape, in which the circulation of fluids is for a time common among the different individuals. The individual animals produced from the stock by gemmation attain to sexual completeness, and propagate by means of ova, in the same manner as the solitary or distinct Ascidiæ do.

The young of these animals undergo a remarkable metamorphosis: they are first excluded from the egg in the form of a moving tailed body, somewhat like a minute tadpole; and this caudal organ of motion is lost previous to their becoming fixed, and the development of the more complex organisation.†

Although the changes to which both the Bryozoa and Ascidian Tunicata are subject in their early state present some very striking phenomena of metamorphosis, yet there is nothing in either which only deserves the name of alternate generation, for all the individuals of which these compound animal structures consist are alike sexually perfect, and there does not appear to subsist any necessary connection between the nonsexual process of multiplication, and the subsequent exercise of the sexual function. There are, in fact, scarcely any intermediate stages of non-sexual existence such as are described in the true instances of alternate generation. It is deserving of notice, however, that Löwig and Kölliker are of opinion that in some of the Botryllidæ numerous embryoes are at once developed from a single ovum by its division, these individuals subsequently multiplying by gemmation into the perfect sexual animals.

Fig. 20.



Bowerbankia densa. (*After Farre.*)

a, one of the animals fully expanded.
b, a similar animal completely retracted.
c, an immature animal.
d, one of the gemmæ in its earliest state.

Salpidæ. — The most marked example of alternating generation among the Tunicata is that which, since its first discovery by Chamisso, in 1819, has been known to occur in the Salpidæ. This process has been so well and fully described in the article Tunicata, that it is not necessary to give more than a short outline of it in this place. These animals are known in two states, viz. solitary and aggregated; the latter being not organically united like the compound polypes, but merely adhering more or less strongly to one another so as to form a chain. The aggregated, but not the solitary kind, possess sexual organs; and it would appear, though this is not yet determined with certainty, that all the individuals of one chain are of a similar sex either male or female.

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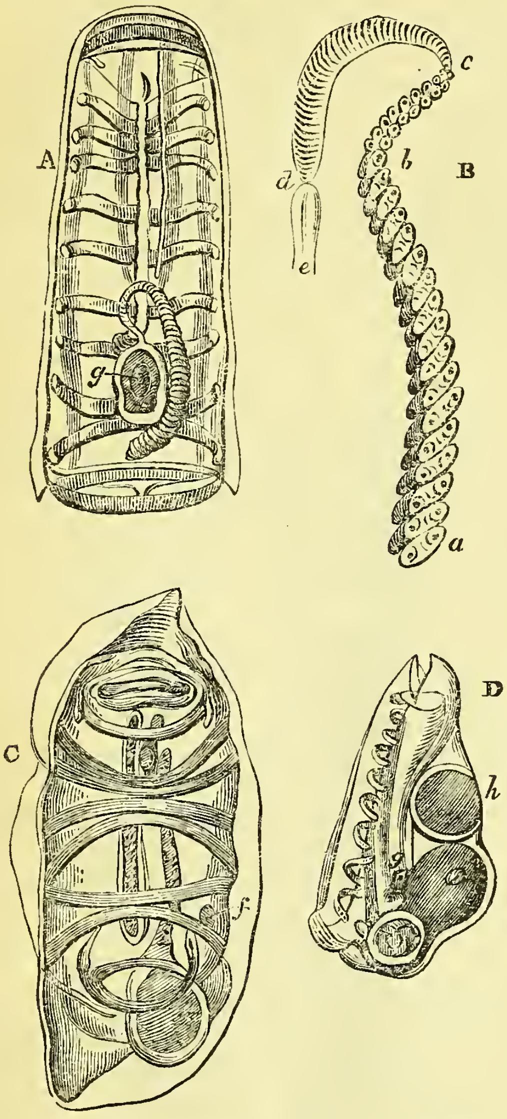
* Van Beneden, in Mém. de Bruxelles, tom. xviii. See the Article Polypifera, for an account of these researches.

† See Mr. Rupert Jones's excellent Article Tunicata for an account of these phenomena, and the special Memoirs of Milne-Edwards, sur les Ascidies Composées, &c., Paris, 1832; Löwig and Kölliker, in Ann. des Sc. Nat. April, 1846; Van Beneden, sur les Ascidies Simples, Brussels, 1847.

Fig. 21.



Solitary and aggregated Salpæ. (*From Sars.*)

A, solitary Salpa, with chain of aggregated ones, budding from it.

B, this chain magnified, shewing the successive sets in different stages.

C, one of the more advanced aggregated Salpæ from a chain, *f*, the place of a fœtus formed by sexual generation.

D, fœtus from another more advanced, magnified; *h*, the yolk, by which it adhered to the parent; *g*, the place of the germ for the aggregated chain.

All the individuals of a chain of aggregated Salpæ are produced from a solitary one by a process of internal gemmation, or gradual development from an internal stolon, or germ-stock, from which they are detached gradually and in successive groups: all the individuals of the chain are contained within a tube, and become united to each other after their development, presenting a series of groups of different degrees of advancement; but the individuals in each group being nearly at the same stage of development.

The distinct or single Salpæ, which, with the exception of the want of the sexual organs, do not differ materially from the individuals of the aggregated chain, are produced from fecundated ova which are developed within the body of the parent. These ova differ from the germs from which the aggregated individuals take their origin in the possession of a yolk, and external envelope. Their development proceeds to its termination within the parent body, and the young Salpa is already provided with the internal stolon for the gemmation of its chain progeny, before it passes into its separate state of existence.

The solitary Salpæ may be looked upon, therefore, probably as incomplete or larva forms, and the aggregated are the fully developed sexual individuals. The generation of this animal, therefore, is precisely an example of that succession of two different kinds of individuals which has been distinguished as alternation of generations; each fecundated ovum of the sexual individuals being developed into an animal which never acquires sexual organs, and which produces by a process apparently of the nature of gemmation, a numerous brood of individuals associated in a chain; all of which are sexually perfect, one set developing only spermatozoa, and the females among them being the producers of the ova, which are the source of the new generation.*

Although no other instances of alternate generation have yet been observed in the class of Mollusca, yet it is possible that modifications of this process may hereafter be discovered. An observation related by Agassiz†, in regard to the development of the ovum in one of the Eolidæ, deserves to be recorded, as it may be found to constitute an approach to the metagenetic process. After having described the usual process of division of the yolk in which the first stages of development consist, and the farther progress of formation in the Eolis, he says, — "But the most curious phenomenon which takes place is this; that the whole yolk does not constantly go to form one single individual. But there may be instances when the mass of yolk, which has been subdivided into cells, is itself divided into two or three or more masses, which grow independently, several individual animals arising from one mass of yolk, which thus divides."

Entozoa.—Among the Entozoa the process of reproduction is effected by very various means. All the Nematoidea, or round worms, are of distinct sexes; and their fecundated ova are developed into the parental form without any metamorphosis of a marked kind, (excepting perhaps in the Echinorrhynchi, the process of generation in which is not fully understood,) nor any intermediate process of gemmation. A few of them, however, appear to become encysted in the parenchyma of organs in their young or undeveloped condition, and some in a form different from the parent, as in the Trichina of the muscles, the so called Filaria of the peritoneal cavity of fishes, and the Vibrio tritici. These encysted Nematoidea have not been observed to be possessed of sexual organs [*], and they are not known to be multiplied by gemmation; it is probable, therefore that, to attain the place of their full development, they must be subject to migrations from one animal to another, either directly or in other ways, as through water and vegetables. The ova of these animals appear to possess a remarkable tenacity of life, as exhibited by their long and obstinate resistance to the noxious effects of external agents. [†]

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* See Savigny, Mém. sur les Anim. sans Vertèb. 1816; Chamisso, De Salpis, 1819; Meyen, Ueber die Salpen; Eschricht, in the Isis, 1842; Sars, Fauna Littor. Norvegiae, 1846; Krohn, Ann. des Scien. Nat. July, 1846; who first pointed out the existence of spermatozoa in certain individuals of the aggregated chain.

† Lect. on Comparative Embryology, Boston, 1849, p. 81.

The Cystic, Cestoid, and Trematode orders of the Entozoa present a more varied process of generation, the investigation of which has of late years attracted considerable attention, and which has led to most interesting results as to the nature and relations of several forms of these animals, which were previously regarded as of a most anomalous kind. The Cestoid and Trematode Entozoa have long been known to possess the sexual organs in the hermaphrodite arrangement, and to produce fecundated ova; while the Cystic Entozoa have been observed to multiply only without sexual organs, and by a process analogous to gemmation, and their first origin has been till lately involved in the deepest obscurity. We shall presently see that many, if not the whole of them, may be either undeveloped or metamorphosed aberrant forms of cestoid or trematode animals. [‡]

This view appears first to have been suggested by Steenstrup, in connection with his researches on alternate generations [§]; and it has since been adopted, in somewhat different forms, by V. Siebold, Blanchard, Dujardin, and Van Beneden, and rendered extremely probable by the researches of these and some other observers. Previous to the adoption of this view, helminthologists, looking upon the Cystic Entozoa as distinct and independent animals, were at a loss whether to regard them as ascertained exceptions to the sexual mode of propagation, or to continue to prosecute their inquiries in the hope of being able to discover a process of generation in them analogous to that prevailing in the greater majority of the animal kingdom; and many were thus misled into the error of searching for ova where none existed or were required. Thus Gulliver erroneously described certain calcareous particles in the membrane of Cysticercus as the ova of the animal [*], and H. D. Goodsir, in his instructive paper on the production of the young in that animal, and in the other forms of Cystic Entozoa [†], failed to distinguish between that which might be merely a process of gemmation and the origin of the embryoes from true ova. [‡]

Cystic Entozoa. — The Cystic Entozoa present themselves in three principal forms, viz. Acephalocyst, Cœnurus, and Cysticercus. The two first are usually found as compound or aggregated animals; the last is more frequently seen in the single or isolated condition.

Some of the vesicular hydatid tumours, constituting the various kinds of so called acephalocysts, have long been known to contain small Echinococci floating in the fluid of their interior. Repeated observations have demonstrated the existence of these animals in the acephalocysts; and it seems very probable that, in the end, it will be necessary to withdraw the distinctions between the various kinds of these cysts, as they will all, by sufficiently accurate observation, be found, at some period of their growth, to contain in a more or less complete condition, the small animals of Echinococci, or their remains. [§]

The Echinococci are produced by nonsexual generation, or by gemmation from the membrane of the vesicle, probably from the middle or germinal membrane, as it has been called by H. D. Goodsir ; and they have been observed, in some instances, attached in pediculated vesicles, singly or in groups, to the inner surface of the cyst.* While enclosed in the pediculated vesicles, the head of each echinococcus is retracted within the short vesicular body in a manner which seems to be general among the young of encysted Entozoa. They are afterwards set free, and in this state are found floating as minute whitish particles in the fluid of the cyst. They then present the appearance of minute heads of Tæniæ, with a short body scarcely larger than the head ; the latter part being furnished with a terminal double circle of hooklets, and four suckers.†

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[*] See a Memoir by V. Siebold, on the Nonsexual Nematoidea, in Wiegmann's Archiv, 1838.

[†] Dr. Henry Nelson and I have observed the development of the ova in Ascaris mystax to proceed for several days, while the parent bodies containing them were immersed in oil of turpentine.

[‡] For a notice of the generation of the minute parasitic animalcule called Gregarina, see the previous account of the reproduction of Infusoria.

[§] See Ray Society's Translation, 1845. p. 100. "It is not unlikely," says Steenstrup, "that in course of time, it may happen with them (Cystic Entozoa), as it has with the whole division of the asexual Trematoda of Siebold, viz. Cercaria, &c., that they must be rejected from the system as being earlier forms of development, or earlier generations of other animals." V. Siebold remarks in a note at p. 157. of his Lehrbuch der Vergleich. Anat. part i. published in 1845, "Here the doubt arises whether the asexual Cystica really deserve to be considered as independent animals. It is very probable that the vesicular worms are undeveloped Cestoids." &c. See also note at p. 111. Von Siebold has developed these views more fully in a recent Mem. in the Zeitsch. für Wissensch. Zool. July, 1850, translated in the Ann. des Scien. Nat. vol. xv. 1851. p. 177; and in the article Parasites, in Wagner's Handwörterbuch der Physiologie. E. Blanchard in his Rech. sur l'Organis. des Vers, in Ann. des Scien. Nat. 1847, vol. vii. p. 120. excludes entirely the Cystica from a separate place in the systematic arrangement, bringing them under Cestoidea, and affirms decidedly that the distinction between them ought now to cease, as they are shown to be different states of the same animals. He refers to De Blainville as having previously entertained the same view. See also Dujardin, in Annal. des Scien. Nat. for 1843, and Hist. Nat. des Helminthes, 1845; Miescher, Bericht üb. die Verhand. der Naturforsch. Gesellsch. in Basel, 1840; and Van Beneden, Ann. des Scien. Nat. 1851. p. 309; and a work on the Entozoa, published at Brussels, in 1850, which I have not seen.

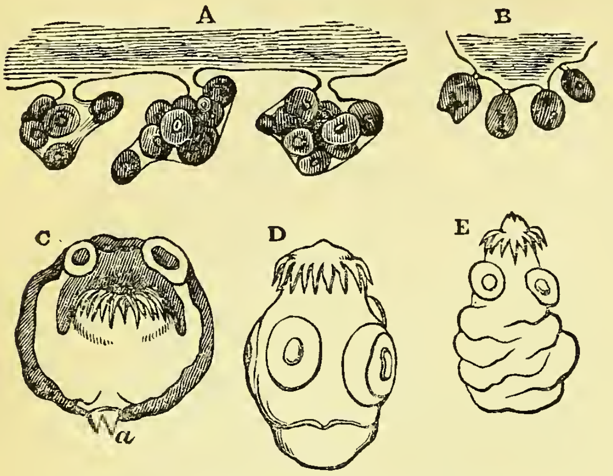
[*] Med. Chir. Trans. of Lond. vol. xxiv. 1841.

[†] Trans. Roy. Soc. Edin. vol. xv. 1844, and in Anat. and Path. Observations. 1845.

[‡] See also Rose, in Med. Chir. Trans. vol. xxxi. 1848.

[§] See V. Siebold's Report on Zoology, in Ray Society's publications, for 1845 and 1847; also Burdach's Physiol. B. ii.

Fig. 22.



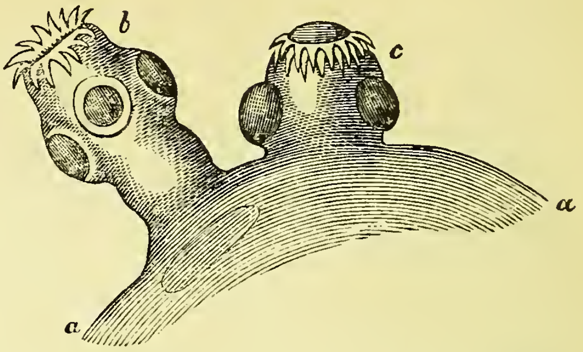
Echinococcus hominis. (*From Wilson.*)

A and B, grouped and single Echinococci, attached by peduncles to the inner membrane of the cyst. C, a contracted, and D, an expanded Echinococcus; *a*, the peduncle. E, a more advanced animal, shrivelled.

The mode of gemmation may probably vary in different circumstances, more particularly in regard to the extent to which the progeny of gemmation may or may not repeat the formation of others of the same kind ; but every thing that is known of the acephalocystic productions seems to point to the view that they are all nearly allied, and that they are abnormal or aberrant conditions of Tænia-larvæ, which, when they become encysted, are incapable of development into the cestoid form which belongs to those that have reached the free intestinal habitation.

The Cænurus, which has been met with principally in the brain and some other parts of the sheep and some other Ruminating animals, consists of a large cyst or vesicle with a number of small heads projecting on its external surface: each head resembles closely that of an echinococcus animalcule, presenting the same circle of hooklets and four suckers. According to H. D. Goodsir, they are attached to the middle membrane of the cyst, from which they sprout at first, carrying the outer one along with them : the neck contains cells, from which it is supposed other young animals or heads may be formed.*

Fig. 23.

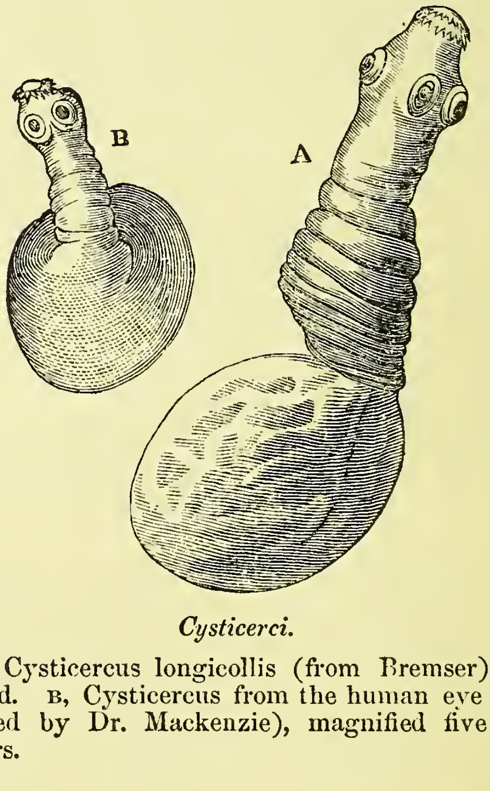


Cænurus cerebralis, magnified. (*After Bremser.*)

a a, part of the general vesicle; *b*, an expanded head; *c*, a shorter head, showing the double circle of hooklets.

The Cysticercus has been described in two forms ; 1st, in its simply vesicular state, and 2nd, in its fasciolated condition, or in its transition, as it may be held, to the cestoid, or tape form. The vesicular Cysticercus has only one head ; but the structure of that part is precisely the same as in the Cænurus and Echinococcus, and, we may add, not far different from that of the Tænia itself. They are usually developed singly, that is each vesicle with one head: but some observers† allege that they have seen internal vesicles near the neck, which they look upon as young, or as a progeny of gemmation in that situation.

Fig. 24.



Cysticerci.

A, Cysticercus longicollis (from Bremser), enlarged. B, Cysticercus from the human eye (extracted by Dr. Mackenzie), magnified five diameters.

The Cysticercus fasciolaris, as it has been observed in the rat and mouse, presents the remarkable fact of a Tænia in various states of development, from the vesicular condition of

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* E. Wilson's paper in Med. Chir. Trans. xxviii. 1845; and H. D. Goodsir, Anat. and Path. Obs.

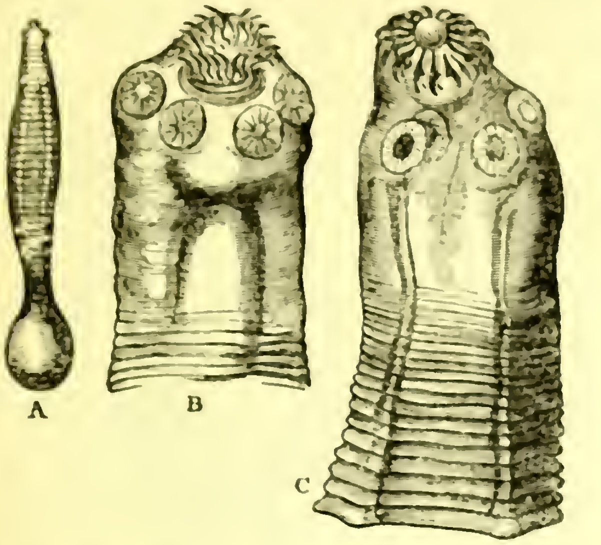
† See Curling, in Med. Chir. Trans. vol. xxiii.; and Müller, in Jahrsbericht of Archiv, 1836. p. 106.

* H. D. Goodsir, loc. cit.

† As Rose and H. D. Goodsir, loc. cit.

the true Cysticercus, to a form in which the caudal vesicle has diminished to such an extent as almost to have disappeared, while at the same time the body has been divided into segments by transverse grooves, as in the Tænia; and in some instances these segments have even acquired sexual organs while the animal was still encysted, a circumstance which has never been observed in any true Cysticercus.

Fig. 25.



Cysticercus fasciolaris of the Mouse, and Tænia crassicollis of the Cat.

A, Cysticercus fasciolaris from the liver of the mouse, natural size. B, the head of the same, magnified. (From Dujardin.)

C, head and first segments of the body of Tænia crassicollis of the cat, showing the double circle of hooks; a few of the smaller under circle being seen where one or two of the larger ones have fallen off.

A close comparison of the structure of the Cysticercus fasciolaris of the rat and mouse in its various stages of development with the Tænia crassicollis of the domestic cat, has shown an almost complete similarity between these animals, and has suggested the view that the encysted Tænia (which the Cysticercus fasciolaris in truth is) may attain its full development as a Tænia in the intestinal canal of those animals which prey upon the smaller Rodentia, in whose liver it begins to be developed in its first simple vesicular form, and gives the greatest probability to the supposition that there may be a similar general relation between the Cystic and Cestoid Entozoa, not of the same animals, but between the tapeworms of different tribes of predaceous animals and the vesicular worms of others serving them as food.*

The different phases of development, therefore, in which the so-called Cysticercus fasciolaris has been seen in the same and in different animals which they inhabit, leave little doubt that they are encysted Tæniæ, which proceed to a much more advanced stage of development than is usual with the vesicular and encysted form of these Entozoa; and we are warranted, from the great similarity of structure, in adopting the view that the true vesicular Cysticerci, the Cænuri and Echinococci, are morbid or metamorphosed and aberrant conditions of the embryoes of various Tæniæ, which may be capable, to a greater or less degree, in different kinds of animals, of multiplying their own incomplete forms by a process of non-sexual gemmation, but which never, in the encysted condition (except in the instances already referred to of the fasciolated kind), attain to sexual completeness; but which either undergo a retrograde change, and thus form tumours and various pathological deposits in the seat of their cysts, or become developed to such an extent as to be injurious or destructive to the animal in which they reside.*

Free Tapeworms. — Three principal forms of cestoid worms are now distinguished from one another, viz. Tæniæ, Bothriocephali, and Tetrarhynchi; the two first have long been known and sufficiently well characterised in their fully grown condition, though little understood in their early or incomplete states; the history of the third, until recently, has been involved in great obscurity, as it has been most variously described by different observers both in the earlier and more advanced stages of its growth. It appears now to be ascertained that all of these cestoids are complete animals, with a single head, a body composed of a multitude of segments, each of which contains male and female sexual organs, which are developed only when the entozoon is living free in the alimentary canal of animals belonging principally to the Vertebrata. The Tæniæ inhabit chiefly the alimentary canal of mammals and birds; the Bothriocephali and Tetrarhynchi more frequently that of fishes and reptiles, and the latter a few mollusca. The Tetrarhynchi have been more frequently described in the encysted and imperfect condition than in the full-grown form, and in such varieties, that V. Siebold has mentioned about sixty different kinds of worms described by various authors under distinct appellations, which might, according to him, be

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* Dujardin, Hist. Nat. des Helminthes, 1845. E. Blanchard (who does not appear to have fully appreciated the necessity of change of habitation for the entire development of the tænia), Sur l'Organisation des Vers, Ann. des Scien. Nat. 1848, tom. x. p. 348. V. Siebold, in Zeitsch. f. Wiss. Zool. 1850, and Ann. des Sciences Nat. 1851. I am indebted to Dr. Henry Nelson, for an account of some interesting researches on this subject which formed a part of his Inaugural Dissertation "On the Development of the Entozoa," on obtaining the degree of M. D. at the University of Edinburgh, in 1850. The limits of this article prevent me from entering into the details of Dr. Nelson's observations, which have not yet been published. It is enough to mention that a very careful comparison of the Cysticercus fasciolaris of the mouse and rat, in various stages of its development, with the Tænia crassicollis of the cat, enabled him to confirm, in a most satisfactory manner, the view which, unknown to Dr. Nelson, had previously been taken by V. Siebold, that these cystic and cestoid forms are different stages of one and the same animal. See also *Leuckart* on Cysticerci, in Wiegmann's and Erichson's Archiv for 1848.

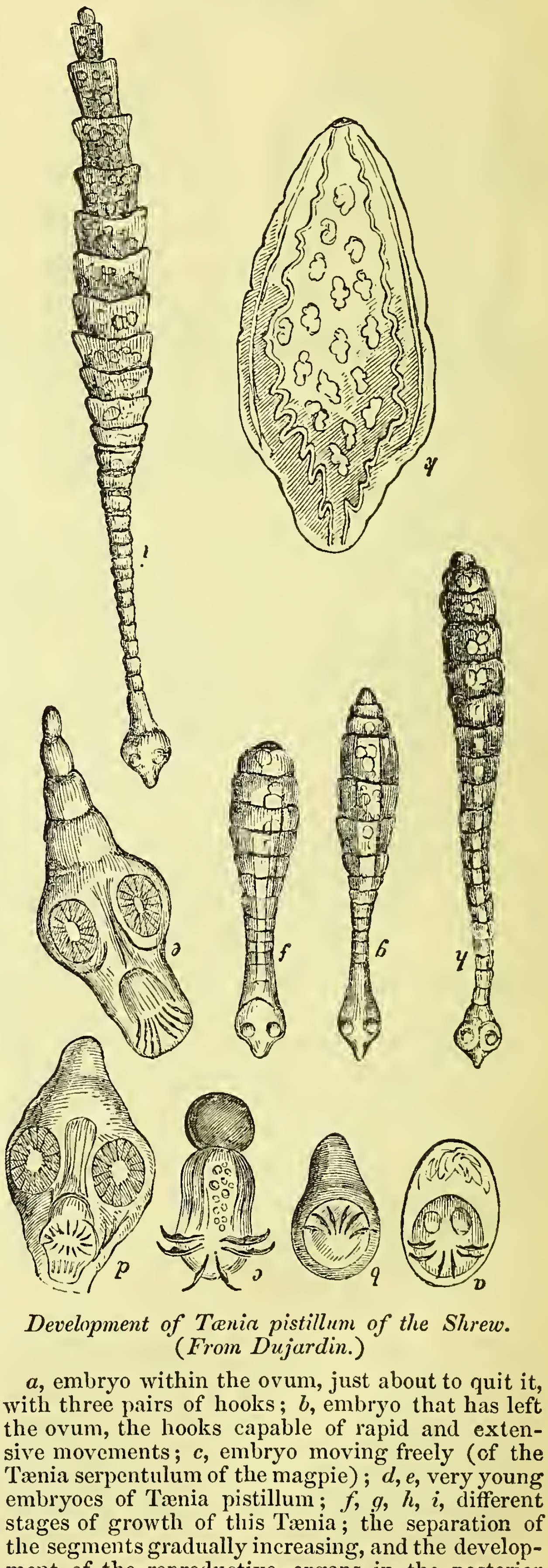
* See Gulliver, in Med. Chir. Trans. 1841.

brought under the genus Tetrarhynchus. In fact, this kind of animal undergoes such remarkable changes in its transition from its first simple Echinococcus-like encysted form to its free segmented sexual Tænia-like shape, that it is not wonderful that its history should have been obscure, and that great doubts should still prevail with some Helminthologists as to its origin, development, and zoological relations.*

It has already been observed, that none of these three kinds of Cestoid Entozoa attain to sexual completeness while they are encysted; and it seems probable that they are all subject, more or less, to migration, in order to gain their free habitation in the alimentary canal of animals, where their segments acquire themale and female generative organs. The fecundated ova, produced in enormous numbers from each segment, do not in general, so far as is known, become developed into embryoes in the intestine of the animal inhabited by the Cestoid, but are evacuated along with the fæces, either separately after being discharged from the oviducts of the Cestoid, or before their discharge by the disjunction of the more ripe terminal segments from the rest of the animal. The migrations to which the ova and young of the Tænioid animals are thus made subject have hitherto opposed so great an obstacle to the observation of their development, that we are as yet in possession of very few continued series of observations in which the whole progress of development from the ovum to the complete segmented animal has been traced. Some important contributions of this kind have, however, recently been made, and the great modifications which the views of comparative embryologists have undergone, from the novel and various aspects in which many of the phenomena of development are to be regarded in instances of alternate generations, have already indicated paths of inquiry by which this very curious and intricate history may ere long be completely unravelled. The accompanying figures from Dujardin's work show the progress of formation of a small Tænia inhabiting the Shrew, and give a sufficiently good idea of the nature of this process in a Tænia, which consists of comparatively few segments (*fig.* 96. *a* to *i.*).

Von Siebold has traced with care a part of the process of development of a minute Cestoid inhabiting the pulmonary sac of the red snail (*Arion empiricorum*) in the encysted condition. Into this situation the minute Tæniæ are introduced from the exterior: they consist of the head with its double circlet of ten hooks each, and four suckers, and a body which is at first entirely destitute of segments, not longer than the head, and forming a soft vesicle, within which (as in other Cystic Entozoa previously mentioned) the head is retracted, so as to give the whole a globular shape. V. Siebold regards it as nearly certain that these minute Tæniæ only attain to their segmented and complete sexual condition when they have been located in the alimentary canal of Vertebrata (Birds and others) preying upon the snails in which the younger forms of the Tæniæ reside.

Fig. 26.



Development of Tænia pistillum of the Shrew.
(*From Dujardin.*)

a, embryo within the ovum, just about to quit it, with three pairs of hooks; *b*, embryo that has left the ovum, the hooks capable of rapid and extensive movements; *c*, embryo moving freely (of the Tænia serpentulum of the magpie); *d*, *e*, very young embryoes of Tænia pistillum; *f*, *g*, *h*, *i*, different stages of growth of this Tænia; the separation of the segments gradually increasing, and the development of the reproductive organs in the posterior ones; *h* (more magnified), the proglottis, or free moving separated segment of this Tænia.

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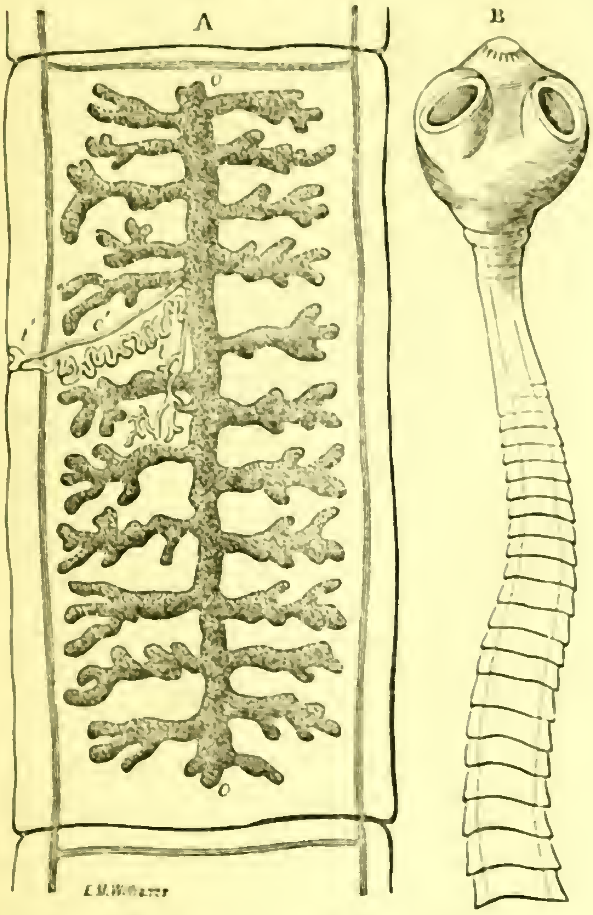
* Von Siebold proposes to substitute the genus Tetrarhynchus for the following five genera distinguished by Dujardin, viz., Rhynchobothrius, Anthocephalus, Tetrarhynchus, Gymnorhynchus, and Dibothriorhynchus. Zeitsch. f. Wiss. Zool. 1850, and Ann. des Sc. Nat. 1851.

The instance already referred to, of the identity of the Cysticercus of the liver of the mouse and rat with the Tænia crassicallis of the cat, and a variety of detached observations which prove that the Bothriocephalus and Tetrarhynchus pass through similar changes from a small Echinococcus-like animalcule to the developed cestoid farm, lead to the corroboration of the same general view that the encysted condition of these Entozoa is an incomplete non-sexual embryo or larva, from which, when it passes into the free state, there is formed by a process of transverse fission a segmented individual or compound animal, in which each segment, as it arrives at maturity, attains to sexual completeness. In this process the new segments are always developed between the head and those already formed. If the character of sexual completeness is to be taken as the distinguishing mark of individuality, each segment of the Cestoid may be looked upon as a distinct animal, and the separation of them by transverse fission may be compared to the separation of Medusa individuals from the Strobila polype stock. The Cestoid Entozoa might in the same manner be considered as subject to a peculiar process of alternate generation.

Fig. 27.



Tænia solium. (*From Blanchard.*)

A, one of the longer mature posterior segments with the sexual organs fully developed; *o, o*, ramified ovary full of ova; *o'*, the oviduct; *t*, the tubular testis; *t'*, the penis, &c.

B, head, neck and anterior recently formed segments.

In the preceding sketch of the nature of the reproductive process in the Cestoid Entozoa, I have followed chiefly the views of V. Siebold as explained in the interesting Memoir already referred to. It is right to state, however, that the phenomena have been viewed in a different light by several observers of high authority. Thus, Blanchard and Van Beneden consider the first stage of the Tetrarhynchus-embryo to be a Scolex, in which, after it has been encysted, the Tetrarhynchus is formed: this, according to Blanchard, is its complete condition; but, according to Van Beneden, the so-called Tetrarhynchus is converted into a Rhynchobothrius, and this is in the last place changed into a separate Trematode animal.[*] Dujardin had previously taken the same view as applied to the separate and independent nature of the joints of the Tænia, which he regarded as individual Trematode animals, and described under the name of Proglottis (see *fig.* 26. *k.*)[†]; but though there may be some points of analogy between the single segments of Tænia and a Trematode, yet the absence of head, differences in the alimentary canals, and other circumstances, render the correctness of this view, at all events, still doubtful.[‡]

Trematoda. — These animals, the most common of which are known as Flukes (excluding the Planariæ), comprehend a set of internal parasites of a structure bearing some resemblance to the Cestoidea, but single, that is, not jointed or segmented. The nervous and vascular systems attain to a considerable degree of development: the alimentary canal, which has a mouth but no anus, is in some bifurcated, and in others more or less ramified. The male and female generative organs are united in one individual, and pervade a large portion of the body of the adult animal.

The facts which have been ascertained in recent times concerning the generation of some of the Trematoda constitute one of the most remarkable parts of the history of this process among the Invertebrata. Their general result may be shortly stated thus: — the fully grown and sexual Trematode animal, as observed chiefly in the Distomata, produces ova, which may pass through the earlier stages of their development either in the viviparous or oviparous mode, more frequently the latter. Each of these ova has formed from it an embryo in which no resemblance to the Trematode parent is to be recognised, but presenting the simple structure of a ciliated animalcule like a polygastric infusorian or a Gregarina. This embryo is

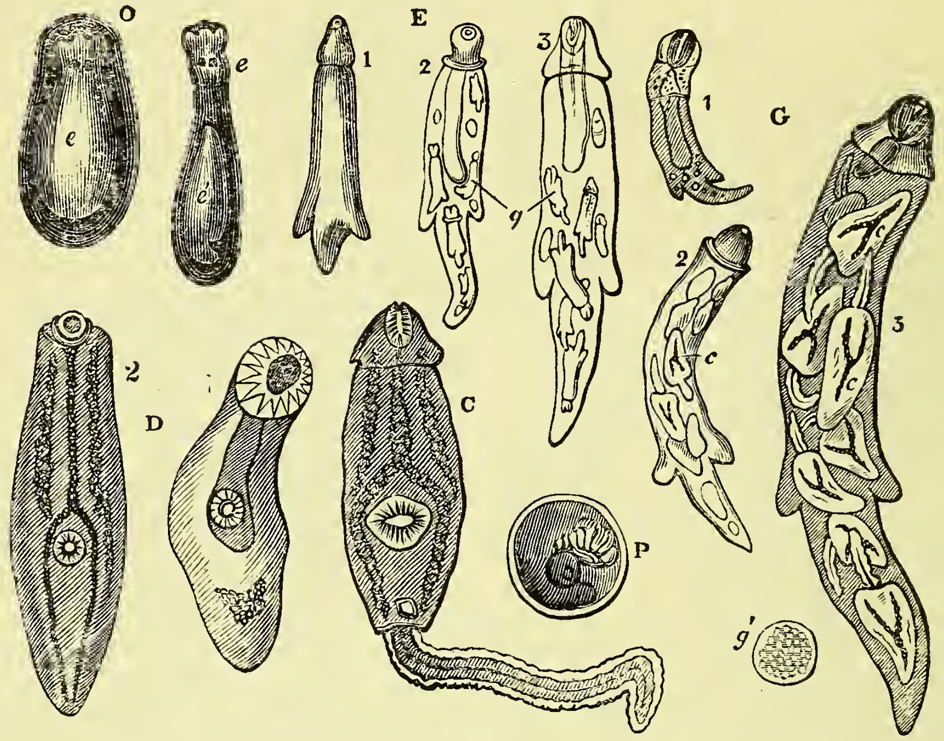
[*] Bull. de l'Acad. Roy. de Belgique, 1849, No. 1., and Ann. des Scien. Nat. vol. xi. 1849, p. 13.; also a work by the same author on the Entozoa, Brussels, 1850, of which I have only seen an extract in a letter addressed to Milne-Edwards, in the Ann. des Scien. Nat. 1851. tom xv. p. 309.

[†] Hist. Nat. des Helminthes, 1845.

[‡] See also Leblond, in Ann. des Scien. Nat. 1836, and Miescher, Bericht Naturforsch. Gesellsch. Basle, 1840; the Works of Rudolphi on Entozoa; the Article Entozoa in this Cyclopædia, by Owen; Kölliker's Memoir on the Development of Invertebrate Animals, in Müller's Archiv, 1843; Eschricht on Bothriocephali, 1840, &c. &c.

not itself converted by any direct process of development or metamorphosis into a perfect Distoma, but has gradually formed from germ-cells within it a progeny, sometimes of one, more frequently a number of bodies, which, when they arrive at maturity, present each one an external form and internal structure and locomotive powers, entitling them to be considered as independent animals. Nor are these directly converted into Distomata; but again there is formed within the body of each, and in the same gradual manner from germ-cells, a new progeny of animals nearly similar to those producing them and equally differing from the complete Distomata. Each of this new progeny, as it increases in size, has formed within it by development from germ-cells the third progeny of the series, and the last of the cycle; but these are different from their immediate parents, and in their internal organisation soon manifest the type of the true Trematode. These animals are endowed for a time with very active locomotive powers, to which a long caudal appendage contributes; their two progenitors have been confined in the parasitic condition, but these are in general freed from confinement, and move about with great vivacity for a time in the water surrounding the animals which their progenitors have infested. In this state they have long been known as Cercariæ, and as they have been supposed to be the young of Distomata, have attracted peculiar notice among Helminthologists.*

Fig. 28.



Series of changes in the development and generations of Distoma. (From Steenstrup.)

O, Ovum with embryo or larva developed in it. *e*, this embryo in a free moving state; *e'*, another embryo in its interior. (These are of Monostomum mutabile, from V. Siebold.)

E, this last embryo farther advanced. 1, first stage, soon after it becomes free; 2 and 3, farther on, with *g*, the second generation, within them in various stages.

G, 1, one of this second generation at an early period of its advancement; 2 and 3, farther on, with *c*, *c*, Cercariæ or Distoma-larvæ, within them; *g'*, one of the granular globules from which the Distoma larvæ and previous generations arise near the posterior part of the body.

C, one of the Cercariæ or Distoma larva with its caudal appendage. P, the same, passed into its encysted or pupa state, having previously lost its tail.

D, Distomata. 1, young Distoma immediately after it has quitted the cyst, and has penetrated a short distance into the body of the snail; 2, Distoma found deep in the viscera.

The free Cercariæ are not, however, directly converted into Distomata; but appear always to undergo a previous metamorphosis in a chrysalis state, or enclosed in a pupa cyst. Previous to the formation of this cyst the Cercariæ adhere to, and bore into, the substance of the animal infested by the Distomata; the tail is cast off, an exudation from their own bodies forms the cyst, which encloses them: within this they remain for many weeks, and even months, moving all the while, and undergoing changes of development, by which they are at last converted into the complete Distoma.

The greater number of the observations from which this remarkable process of generation has been ascertained to occur are due to V. Siebold and Steenstrup; but the whole succession of changes has not yet been observed in any one species, and it is to the latter observer especially that the scientific world is indebted for the ingenious combination and interpretation of the scattered observations of previous inquirers, as well as the addition of new facts, from which an almost entire certainty is acquired that the various phenomena do actually succeed each other in the order above stated, and that the occurrence of alternate or intermediate generations in these animals is established.

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* Nitsch, Beitrag zur Infusorienkunde, &c., Halle, 1817; Bojanus, in Isis, 1818; A remarkable and interesting series of papers by V. Baer, in Nov. Act. Nat. Curios. 1826, vol. xiii.; Rud. Wagner, in Isis, 1834; V. Siebold, in Burdach's Physiol. vol. ii. of German edit. p. 187., or vol. iii. of French transl., p. 32., &c.

Von Siebold had in 1835 described in the Monostomum mutabile the development of the first embryo from the ovum in the Gregarina-like or animalcular form, and had shown the next change to consist in the formation within the first embryo of a second body endowed with locomotive power, and independent vitality, and differing both from its immediate parent and from the adult.* V. Siebold, as well as others, had ascertained the Cercariæ to be themselves incomplete animals, and to proceed from others by a process of internal production of a non-sexual kind. Steenstrup therefore directed his attention particularly to trace these Cercariæ on the one hand, in their development into complete Distomata, and on the other, backwards through their progenitors towards the first origin from an ovum. His observations were made principally in three kinds of Cercaria, which, along with their antecedent and succeeding conditions, are found in great numbers in the fresh water snails, Lymneus stagnalis, Paludina vivipara, Planorbis, &c., and which had been previously named Cercaria echinata, C. armata, and C. ephemera. In these, especially in the first, the conversion of an encysted Cercaria by metamorphosis into a Distoma, and the descent of the Cercaria (by metagenesis) through two progenitors, not themselves Distomata, was ascertained, but he did not succeed in tracing these bodies back to their origin from ova. By a comparison, however, of the body formed within the animalcular embryo of the ovum of the Monostomum mutabile, as observed by V. Siebold, with the first progenitor of the Cercaria, to which it was found to present a remarkable similarity, the chain of evidence seemed to be complete, and Steenstrup found himself in a position to announce the general views of alternate generation, which have ever since their first publication attracted the greatest attention, and contributed in a powerful degree to modify and direct the investigation of the generative processes in the lower animals.

To the immediate progenitor of the Cercaria Steenstrup gave the name of nurse (altrix, Amme), in allusion to its nursing or nourishing function, and to the immediate progenitor of this one he gave the appellation of "parent or grand-nurse." These terms may be objectionable, but an unnecessary amount of criticism seems to have been bestowed on them by some writers. They are adopted hypothetically by Steenstrup; they do not appear to withdraw him from the matter-of-fact statement of his observations; and they seem to be, in many respects, short and convenient terms in the description of the phenomena. These bodies have in the Cercaria echinata all the appearance of distinct animals, that is, a body with a head separated by a neck or collar, a tail or caudal projection, and two processes of the integument similar to limbs, a mouth and alimentary cavity, and they move with all the appearance of spontaneity; but it ought to be remarked that the form and powers of these nursing or formative cases differ considerably in various other species, and in some present so little of the external form or endowments of an independent animal, that the more general appellations of germ-cases, or germ-sacs, or sporo-cysts, may be more appropriate to them.*

It is chiefly among the aquatic Gasteropod Mollusca, and a few land ones, that these observations have been made; but V. Siebold has extended them to some of the Trematoda inhabiting the air-sacs and other parts of water fowls, which no doubt come from the same Mollusca, and obtain access to the seat of their final parasitic habitation from the water or along with food, into which they have come as Cercariæ, after having previously been parasitic in the Mollusca. It is easy to understand how the ova of the Distomata discharged from the bodies of the water fowl may gain their place in the Mollusca. V. Siebold has observed in a very interesting manner also the passage of the Cercariæ into the bodies of water insects (larvæ of Ephemera and Perlida), which he placed together with a quantity of Lymneus stagnalis, from the various parts of whose bodies the Cercariæ were discharged in numbers out of their nursing capsules: the penetration of the integument of the insect by the Cercaria and the mode of casting its tail being precisely the same as that observed by Steenstrup in the Mollusca.†

Both these observers agree that the first and second germ-cases (or nurses), and the Cercariæ, or Distoma-larvæ, arise by a process of gradual development from extremely minute granular spherules, which are at first situated in the posterior region of the body, or between the alimentary cavity and the integument. These are certainly not ova: but we are at a loss to state to what class of reproductive germs they may be referred with greatest accuracy.‡

It is known that the bodies which inhabit the aqueous chamber of the eyes of many fishes are imperfect Distomata. Steenstrup has frequently observed these larvæ in the pupa state adhering to the inside, and sometimes to the outside, of the cornea, and he has occasionally noticed a delicate streak through the cornea, indicating the track through which the animal has penetrated; and he considers it as extremely probable that all the Trematoda of the eyes of fishes, of which a vast variety has been described by Nordmann§, are at one time encysted, and that of the two principal forms distinguished by that observer, the one is the more advanced and the other is the larva.

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* See Wiegmann's Archiv, 1835.

* See Victor Carus, über den Generations-wechsel, for a figure of these more simple forms of sporo-cysts.

† See the Article PARASITES, in R. Wagner's Handwörterbuch der Physiologie.

‡ See *Fig.* 28. *g*.

§ Mikographische Beitrage, &c., 1832.

From what has already been observed it seems probable that other productions previously described as Entozoa of various kinds, may, in reality, be nurses or larvæ of different Distomata; and that many of these may be brought under their several specific distinctions, when the new paths of investigation pointed out by the suggestions of Steenstrup and V. Siebold have been diligently pursued.

Von Siebold has recently related* a very interesting observation on the remarkable double Trematode animal, discovered and described by Nordmann†, under the name of Diplozoon paradoxum, from which it seems to be ascertained that this double animal is produced by the actual union of two nearly similar simple ones, by a process of partial fusion, which, though much less complete, seems to partake in some degree of the nature of conjugation, such as occurs in the Closterium and some of the lower vegetable bodies. The single animal, first described by Dujardin, under the name of Diporpa ‡, was observed infesting the minnow (Leuciscus phoxinus) in the same streams with the gudgeon (Gobio fluviatilis). This animal corresponds nearly in form and structure with the half of the Diplozoon, with the exception of its smaller size, and the absence of generative organs. On the side of the Diporpa a projecting sucker exists, and the union between two of these animals which gives rise to the Diplozoon, begins by a mere adhesion of this sucker, which becomes more and more complete, so as at last to lead to that entire fusion and combination of the adjacent parts of the intestinal canal and some other organs, which has excited so much surprise in the Diplozoon. The development of the genital organs in both of the two united animals succeeds to this union.

Annelida. — Some phenomena in the reproduction of the Annelida are to be referred to the indirect mode of generation now under consideration. The most of these animals are hermaphrodite; they are all more or less jointed, or formed in the adult of repetitions of segments of similar structure, the anterior and posterior alone differing from the rest. The jointed structure does not exist in the embryo when it first leaves the egg; but is gradually produced by a process of gemmation, which may be styled intervening rather than fissiparous. In the multiplication of these segments the new ones are always formed in the interval between the caudal segment and that which is next to it; the seat of new production differs therefore in the Annelida and Cestoid worms; for in the latter of these animals the new joints are developed at the cephalic extremity, and there is also some difference in its nature, as the multiplication of joints in the Tænia is in some degree truly fissiparous.

A few of the jointed Annelida have long been known to be subject to another kind of development, by which one or more complete segmented individuals are formed close to their caudal extremity, and spontaneously separate to enjoy for a time an independent life. This remarkable fact was first described by Otto Fred. Müller, in the small Nais proboscidea*; and Gruithuisen described accurately the same phenomenon in a Nereis or Chætogaster.† This process was looked upon by these observers as an instance of accidental fissiparous generation; but it has received a different signification and a greater interest from the more recent researches of Quatrefages and Milne-Edwards.

The first of these naturalists observed in a number of individuals belonging to the genus Syllis‡, at a certain period of their life, a new individual to be formed at the caudal extremity of each. The part was first marked off by a notch or transverse groove, the form of the parent individual gradually appeared in it, with the head, eyes, the same joints, limbs, &c., and it was ultimately separated by spontaneous fission. But the resemblance between the original individual and its offspring was chiefly external; for it was found that while the parent animal continued to exercise as before the functions of nutrition it was not possessed of generative organs; and, on the other hand, the new individuals seemed destined alone to perform the reproductive functions, and contained the fully formed sexual organs, while their alimentary canal appeared to become atrophied, and was not employed in the digestion of any newly assumed food. These individuals lived long enough after separation to complete the reproductive process by the formation of fecundated ova.

Milne-Edwards observed in the Myrianida fasciata §, a similar, but more numerous gemmiparous production of sexual individuals. In this animal, as many as six new individuals were observed to be formed in gradual succession, one before the other, and between the caudal and terminal segments of the original body. Each one of these new individuals, as it

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* Zeitschrift für Wissensch. Zool. 1851.

† Op. cit.

‡ Hist. Nat. des Helminthes, 1845. Dujardin had noticed the resemblance between this body and the two parts of the Diplozoon, and had conjectured that it might be in some way the young of the Diplozoon.

* Naturgesch. einiger Wurmarten des Süssen und Saltzigen Wassers, Copenhagen, 1800; and in a Nereis, in Zoologia Danica.

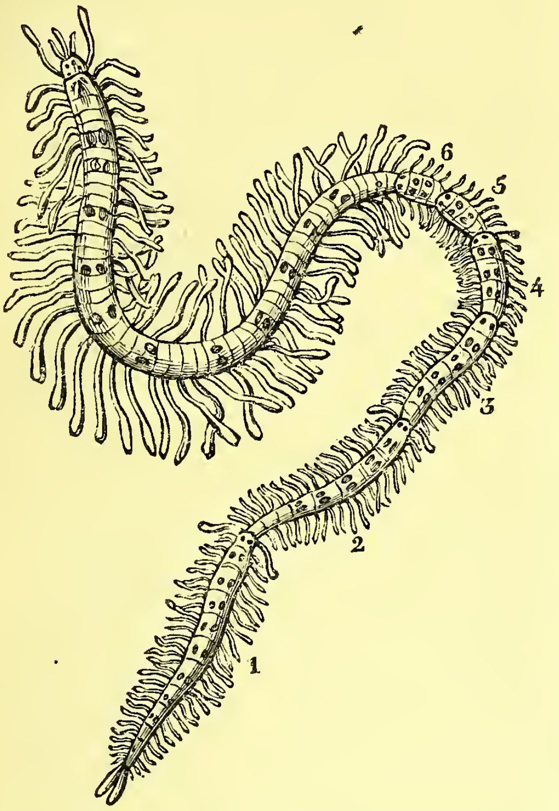
† Nov. Act. Nat. Cur. vol. xi. See also J. Müller's Physiol., by Baly, vol. ii. p. 1424; Owen's Lect. on the Gener. and Develop. of the Invertebrated Animals, in 1849, in Med. Times, vol. xx. p. 83, where he refers also to observations of Oersted in an Eulosoma, and of Schmidt in a tubicolar Annelide, called Filograna.

‡ Annal. des Scien. Nat. 1844, tom. i. p. 22. Otto F. Müller had also noticed the phenomenon in the same animal, and described it under the name of Nereis prolifera, in his Zoolog. Danica, vol. ii. p. 15.

§ Annal. des Scien. Nat. 1845, tom. iii. p. 170. See also Longet's Traité de Physiologie, tom. ii. part 3rd, p. 47.

arived at maturity, and acquired the external configuration and structure (though of smaller size) of the parent, was found to be possessed of reproductive organs, while the original animal had not acquired any. The first formed was situated farthest back, and remained for the time attached to the original caudal joint, and the others followed in succession before it, the last produced being attached to the terminal joint of the parent body; and each newer individual presented a less developed structure than the preceding one. In the animal observed by M. Edwards, the anterior or youngest individual had only ten rings, the second had fourteen, the third sixteen, the fourth eighteen, the fifth twenty-three, and the last, or caudal one, thirty rings. It would appear, therefore, that the new individuals take their origin from the last joint of the parent Annelide. The observations of M. Edwards farther make it appear that the process of development and multiplication of the segments in each of the new individuals is the same as in the young Annelide first formed from the ovum; that is, the embryo is at first without segments or rings, the head and caudal part existing alone, and the joints being gradually formed between them, and in succession from the posterior of the segments previously produced.

Fig. 29.



Myrianida fasciata. (*From Milne Edwards.*)

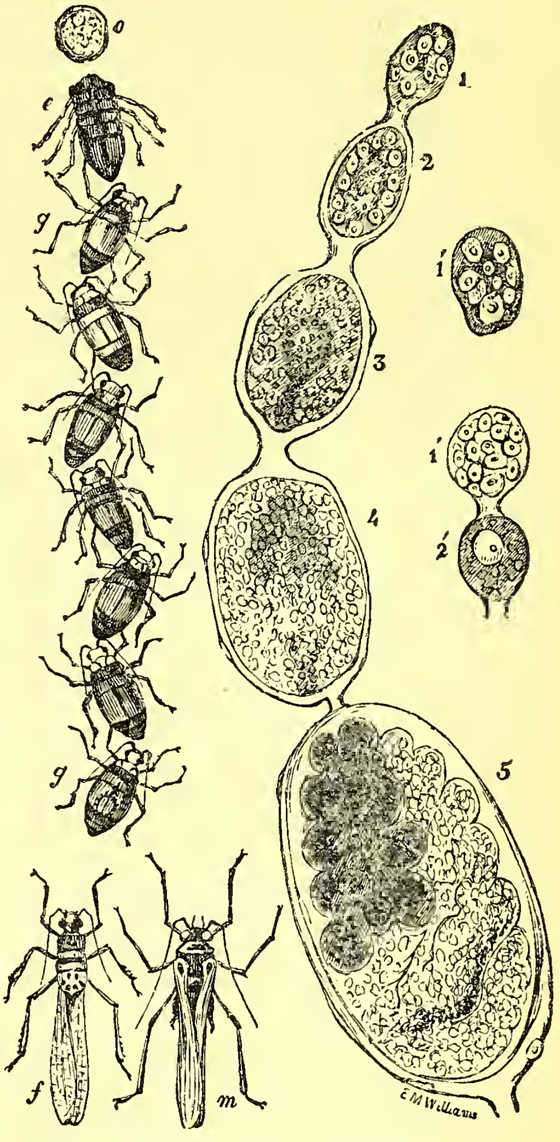
Twice the natural size. At the posterior part of the body are seen six young, produced between the caudal and the next joint in succession, from 1 to 6.

These phenomena cannot fail to recall to our recollection the production of sexual individuals by a non-sexual process analogous to gemmation from imperfect parents or nursing stocks; and as Mr. Owen has remarked*, "Since the individuals so propagated alone acquire the generative organs, an alternation of generations may here be affirmed of such species; the oviparous individuals producing eggs from which the gemmiparous individuals come, and these, in their turn, reproducing the oviparous individuals." †

But it is to be observed, that in many others of the Annelida, the generation is of the ordinary kind, or consists in the production of sexual individuals, by their direct or metamorphic development from the ovum.

Insecta. Aphides. —A remarkable example of a similar modification of the reproductive

Fig. 30.



Production of Aphides.

A. (*After Owen.*) Diagrammatic representation of the succession of generations of Aphides, from the fecundated ovum *o*, the first embryo *e*, the successive non-sexual progenies, *g* to *g* (of each of which only one individual is represented), to the male and female insects, *m* and *f*.

B. (*After Leydig.*) Enlarged view of the chambers of one of the ovarian oviducts of a viviparous Aphis. In the uppermost chambers are seen the fine nucleated cells, of which one in 1′ and 2′, larger than the rest, descends; and in 3, 4, and 5, are seen the changes of this and other granular and cellular blastema, from which the new individual is formed.

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* Lectures, 1849, Med. Times, vol. xx. p. 83.

† At the same time it ought to be mentioned in connection with the above, that, according to some

process among animals higher in the scale, but in them of an exceptional character, has long been known to occur in the various species of the common plant-louse, or Aphis, first discovered by Reaumur* and Bonnet†, and confirmed and more fully illustrated by a variety of accurate entomologists in more recent times. In this aninal, successive generations, amounting each to a considerable number, and in the Aphis lanigera‡ averaging about a hundred, are produced for seven, nine, or eleven times, according to the species, from parents of no sex, or rather which seem to possess the structure of females imperfectly developed. The course of the generative process is the following: perfect male and female winged insects are observed only towards the autumn season: these fly about in great quantities, the impregnated females deposit their eggs, covered with a protecting case of mucous in the axils and other recesses of plants, where they remain during the winter. In spring, there are developed from these ova, a brood of larvæ, or imperfect female Aphides, which soon produce, by an act of viviparous generation, and without any concurrence of the male sex, a progeny of a similar kind, and this is repeated, in successive generations, for nine or ten times in the common species, or for ten or twelve weeks during the summer, at the end of which time the last brood brings forth male and perfect female individuals, both of which die after having provided by the production of fecundated ova for the continued generation during the next season.

Upon the discovery of this very remarkable mode of reproduction, various theoretical conjectures were made in regard to its nature; but no satisfactory explanation presented itself, till the knowledge of the general nature of the process of non-sexual larvation came to be brought under a general principle or law. It is now obvious that the production of the successive generations of Aphis-larvæ may be regarded as an instance of the multiplication of individuals from the product of a single ovum, previous to the development of the true sexual organs and the exercise of the sexual functions. But this example of non-sexual larvation deserves attention, not only from its occurrence among animals placed so high in the zoological scale of organisation as insects, but also from the degree of perfection of the larvæ themselves, and from the circumstance that the new broods are formed, not as in the other examples of this process to which the attention of the reader has already been directed, by a division of the whole body, or by gemmation from its external or internal substance, but from germs arising within a determinate organ, corresponding in its general form and anatomical relation, though not entirely similar, to the generative organ of the perfect female.*

The genital organs of the viviparous or larval Aphides differ from those of the perfect or oviparous females, principally in the want of the receptaculum seminis, and the organ which secretes the mucous investment for the ova, and there is also some difference in the form of the ovarium, or germiparous part of the organs.†

The gradual development of the larva brood within the oviduct of the viviparous parent has been traced carefully by several observers. J. Victor Carus has attempted to show that this process is to be distinguished from the usual process of development from an ovum by the absence of cell multiplication, and by the formation of the embryo of the larva from a merely granular germ; but more recently Leydig ‡ has shown that though there may be differences in the structure and mode of development of the ovum and of the viviparous germ, the latter arises as truly as the former from cellular elements. The uppermost compartment of the oviduct contains, according to Leydig, from eight to twelve distinct nucleated cells, together with a quantity of finely granular substance. One of these cells appears to descend into the second compartment, in which an outer layer of cells exists, with finely granular substance internally; in the third compartment the cells of the outer layer have become still smaller and more numerous, and have formed, in fact, a covering to the germ, similar to that which proceeds from cleavage in the ovum. The rudiments of the internal organs now begin to be distinguishable, and the various external organs are successively developed out of the cellular mass. The cellular structure of the ovum of insects is at all times difficult to be traced in the earlier stages of development; and it seems to be established by these observations that the origin of the embryonic structures from cells is at least as obvious in the viviparous as in the oviparous germ (see *fig.* 30. B.).

General Remarks on Alternate Generations.— Having now shortly described the principal varieties of the reproductive process which may be brought under Steenstrup's law of "Alternate Generation," it may be proper to review very briefly their general nature.

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recent observations, the parent or stock individuals of both Syllis prolifera and Nais proboscidea arrive ultimately at sexual perfection after having given off a number of sexual individuals by the caudal gemmation. See Leuckart on Metamorphosis, Non-sexual Reproduction, and Alternate Generations, in Zeitsch. für Wissensch. Zool. 1851, in which he refers to Frey and Leuckart, in Beitrage zur Kenntniss Wirbellos. Thiere, p. 96.; and to Schultze, in Archiv. für Naturgesch., 1849, p. 287., for observations proving this fact.

* Histoire des Insectes, tom. iii. Paris, 1738.

† Traité d'Insectologie, ou Observations sur les Pucerons, 8vo, 1745.

‡ See Owen's Lect. on the Invertebrate Animals, 1843, p. 235.

* It is conjectured by Von Siebold (Vergleich. Anat. der Wirbellos. Thiere, p. 634.), that the same mode of production may occur also in some kinds of Cynips and Psyche.

† See the interesting observations of Owen, in Parthenogenesis, p. 38., and elsewhere; V. Siebold, Vergleich. Anat. and Froriep's Neue Notizen, vol. xii. p. 308.; and J. Victor Carus, Zür nähern Kenntniss des Generations-Wechsels, Leipzig, 1849.

‡ V. Siebold and Kölliker's Zeitsch. für Wissenschaftliche Zoologie, vol. ii. p. 53.

These phenomena are confined to the Invertebrated animals, and among them are to be regarded as occasional and exceptional rather than general. Among the Protozoa they may exist to a greater extent than is yet known; they occur more or less in all the divisions of the Radiata, but more constantly and obviously in the Polypina and Acalepha than in the Echinodermata: among the Mollusca they have been observed only in the comparatively limited classes of Bryozoa and Tunicata: they are almost universal in two divisions of the class Entozoa, viz. the Cestoidea and Trematoda, but they are altogether absent in the Nematoidea; they belong only to the lowest division of the Annelida, and among the Articulata proper the almost entirely exceptional examples are confined to the class of insects. Nor are the phenomena universal in those classes or orders of the animal kingdom in which they have been described. In some of these divisions, therefore, and in all the others of the animal kingdom, the manner of the reproductive process is ascertained to be *direct*, that is, by generation from sexual parents, and by development, or in some instances by metamorphosis, from ova to sexual individuals; to which may be added in some animals, by the multiplication of like individuals, separate or aggregated, by gemmation. But although this general statement is applicable to the present state of our knowledge, we are still too imperfectly acquainted with many forms of the reproductive process to warrant us in affirming that there may not yet be discovered many other deviations from that which has long been familiar to our minds as the more common and direct connection between the ovum and the perfect or sexual individuals which produce it. In the mean time let us endeavour, according to our present information, to determine the true character of the seemingly exceptional phenomena, of which the more important have been noticed in the preceding section.

The views first suggested by Steenstrup, in 1842, in connection with these phenomena are unquestionably to be regarded in the light of a discovery, and the attempt to deprive them of their character of novelty and importance, or to refer them to other previously known general laws, has entirely failed.* It may be that the smaller portion only of the facts on which the views are founded may have been first observed by Steenstrup, and that parts also of these views may be in themselves premature, speculative, or erroneous; but all discoveries in science are the result of the successive and concurrent observations of a number of inquirers; and no one who has had an opportunity of studying the history of the progress of research into the reproductive function during the last twenty years, will deny that the view which has associated together the phenomena in question under a common principle, has had a most important influence in modifying the doctrines and in guiding and suggesting the researches of those physiologists who have devoted themselves to inquiries into the origin, early conditions, and zoological affinities of the lower animals; and it may truly be affirmed, that no one could at present enter upon the investigation of any obscure or doubtful department of animal or vegetable production among the lower series of these kingdoms of nature, without making especial reference to the views embodied in Steenstrup's generalisation.

The occurrence of non-sexual multiplication among some of the Invertebrated animals had long been known, as of Polypes, by budding, so admirably described by Trembley in his work published in 1744; and of the Aphides, by internal production, discovered by Reaumur and Bonnet; and of the Nais and Nereis by external extension, described by Otto F. Müller, in 1800; the imperfect conditions of some of the Entozoa had been detected by Nitsch and V. Baer in 1818: the two forms of the Salpæ were known to Chamisso in 1819, who, more than any other observer, appears to have foreseen in these animals the discovery of alternate or dissimilar generations; but the first observations, from which the peculiar nature and general doctrine of the phenomena now under consideration may be regarded as having been deduced, are those of Sars, on the compound Polype stock of the Medusæ, in 1828, and of Rud. Wagner, on the production of Medusiform bodies from a polype (Coryne aculeata), in 1833. From that time, observations followed one another in rapid succession, and continue still to crowd upon us, so as to have changed almost entirely the aspect in which we have been accustomed to regard the development of the lower animals: and it is only necessary to mention collectively the names of some of those whose observations have contributed most to extend and to establish these discoveries in different classes of animals, to exhibit the importance attached to them by zoologists, comparative anatomists, and physiologists of the highest character in our time, such as Dalyell, Lister, Sars, Lovén, V. Siebold, Nordmann, Eschricht, Steenstrup, Van Bénéden, Kölliker, Owen, Dujardin, Milne Edwards, Blanchard, Quatrefages, J. Reid, J. Müller, E. Forbes, Désor, Vogt, Agassiz, Huxley.

The peculiar nature of these phenomena as compared with those of the better known and more common form of sexual generation, consists in this, that in some animals, in all of which, be it observed, the permanence of the species is secured by the sexual production of ova, the body or individual which is developed immediately from the ovum is not, in general, itself the bearer of the sexual organs, but, nevertheless, maintains for a time an independent existence, or presents the structural and functional characters of a separate or distinct individual; these characters often differing remarkably from those of the sexual individuals from which the ovum derived its origin : and that subsequently this individual, or one or other of its successors, has formed in connection with it, either internally or externally, and without sexual organs, a new progeny, which may consist of one or of many individuals, which have each of them more or less of the structure and properties of independent animals, and which, however variable their other organisation may be, present this in common, that they are sexually complete, and renew the true generative act by the formation of fecundated ova. In some animals it is the immediate offspring of the individual developed from the ovum which resumes the sexual function ; in other animals this offspring bears a second brood, or a third, and even more successive generations, before the return is made to sexual reproduction. This process of non-sexual production is in some instances, very analogous to external gemmation ; in some it resembles transverse fission ; and in others it proceeds from the interior of the parent body, in a manner which has been called internal gemmation, but which must be considered as different from a true budding process, and cannot, in a few words, be correctly characterised. These deviations, therefore, are peculiar in this, as compared with the mode of reproduction in other animals ; viz. 1st, that the immediate product of development from the ovum is not usually itself the producer of ova, but that this function is delegated as it were to the sexual individuals, which are the products of its non-sexual generation ; 2nd, that it frequently happens that in place of one individual only resulting from the development of an ovum, several, and even a great multitude of individuals are produced by the non-sexual multiplication of the product of sexual generation ; and, 3rd, that while the several series of individuals proceeding from the various successive acts of production, may, in one sense, be regarded as different stages of an animal specifically the same, or are together necessary to make up the species, yet their form, organisation, and modes of life are often so different, that many of them have frequently been described as belonging to different species and genera, or even to different orders and classes of animals ; and, but for the knowledge now possessed of their close affinity, as established by their common origin, would still continue to be dissociated from each other in the systems of the zoologist.

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* See Ed. Forbes' Remarks, in Treatise on Naked-eyed Medusæ, 1848, p. 83., *et seq.*

The doctrine of alternating generation has not, however, been admitted without reservation by some physiologists. In various parts of his recent admirable work on General and Comparative Physiology, and elsewhere *, Dr. Carpenter has expressed his dissent from the views of Steenstrup, both as regards the existence of an alternation of a true generative process and the alleged *nursing* function of one or more of the series of individuals so produced; and seems disposed in some measure to undervalue that author's researches, considered either as original observations, or as embodying a novel and important generalisation. Dr. Carpenter regards the phenomena in question as analogous to, if not identical with those of metamorphosis rather than of generation ; and we are left to suppose that he does not think the difference essential between such metamorphoses as occur in one and the same individual and those which result in the production of a multitude of dissimilar individuals. According to this view, the new animal produced by the non-sexual process is the result of a process of development or growth, and ought therefore to be regarded as formed by budding or gemmation, rather than by an act of generation properly so called. In a recent paper on the subject of Metamorphosis, Non-sexual Reproduction, and Alternate Generation (Zeitsch. für Wissensch. Zool. June, 1851, p. 170.), Leuckart has advocated somewhat similar views, endeavouring to refer all the instances of so-called alternate generations to metamorphosis ; but this obviously requires that we should change the signification usually given to this term. But the restriction of the word generation to the sexual process of reproduction, though it might be convenient and proper, were we now to have to employ it for the first time, seems somewhat arbitrary in this case, as it is contrary to common practice, and physiologists have long been in the habit of making the distinction between sexual and non-sexual generation. No new term has been suggested applicable to, or descriptive of, all the phenomena in question ; and I apprehend, that, however desirable the change may appear, we must continue to designate the process of non-sexual production as one of "Generation" in its physiological sense, and the series of new beings thus formed as so many "generations" of individuals in the common or vernacular sense of the term. As Professor E. Forbes remarks, the alternation of forms is admitted, but not the alternation of generations. The bodies produced by one individual, if they assume new forms and move about as separate and independent animals, must be regarded as so many distinct individuals ; and if they are different, and if the one produces the other (even though it may be by a process of gemmation), we must admit that they belong to different generations.

The distinction between the formation of a new individual from an impregnated ovum, and that which takes place without the concurrence of sexual organs, is one which, unquestionably, all will feel disposed to regard as most important ; but it still remains undemonstrated that all the animal beings which are of non-sexual origin are necessarily formed by a process of gemmation analogous to ordinary growth. It has already been pointed out that the mode of their origin is, so far as it has yet been ascertained, very various ; and, at all events, in some of them, there is a wide departure from that which we have been accustomed to regard as an act of gemmation, or simple sprouting of the parent texture. We cannot be too cautious in making wide generalisations in regard to phenomena so various and so imperfectly known as those of alternate or intermediate generation are; and the only safe course in the progress of such inquiries is to apply terms to the phenomena which are no more than the exact expression of what is well ascertained regarding their nature. Now, who that has observed or studied the history of the two states of the Salpians, and the relation in which they stand to each other, can hesitate to admit that two dissimilar generations alternate, and that a different generative process has taken place for the production of each? or who, knowing the relation subsisting between the fixed marine polype and its free moving medusoid offspring, or that between the larger medusæ and their compound polype stocks, would deny to each of these series of beings the attributes of distinct individuals, or regard the productive acts by which they take their origin in any other light than as two dissimilar kinds of generation? But this seems scarcely more than a question of words. It is important rather to notice that while some of the polypes now alluded to multiply their like (that is polype-forms) by budding, their medusoid progeny also occasionally produce their like (or similar medusoids) by gemmation; and surely it is expedient to regard as somewhat different that production of distinct medusoid individuals from a polype stock, which is an advance in its stage of being, and which gives rise to an animal different in structure, mode of life, and functions, from its parent, from that kind of production which is no more than the repetition of the parental form or the extension of its parts.

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* In the British and Foreign Medico-Chirurgical Review vol. i. and vol. iv.

The term *nurse*, applied by Steenstrup to the non-sexual producers, seems inappropriate, and may, in one part at least of his treatise*, have led him into purely speculative comparisons, such as that with the workers among the gregarious insects; but in other parts of his essay the author's speculative views are kept in strict subordination to the simple description of the facts. Due allowance ought also to be made by the English reader of this work, for the circumstance that, though an excellent translation, it comes to him through the German from its original language. Less objection would probably have been taken to his theory had the term "preparing stocks," or some one conveying a similar meaning, been substituted for that of "nursing individuals."

Professor Owen also, though admitting in the full extent the peculiar and important nature of the phenomena of alternate generation, objects to the term nurse or nursing animal, as calculated to mislead, and holds the views of Steenstrup, embodied in the phrase "Alternating Generation," to be defective, as not affording any real explanation of the nature of the phenomena, or rather, as being no more than a statement of the facts, without referring them to a sufficiently general law or connecting principle.

Professor Owen's attention had been, before 1843, attracted to the remarkable non-sexual multiplication of the summer Aphides, the structure of which he minutely examined, and had been led to the opinion* that the germs from which the offspring of this non-sexual generation arises are the remains of the original germ-substance of the yolk, which have not been applied to the formation of organised textures in the individual immediately developed from the ovum. Professor Owen has given the name of Parthenogenesis, or Virgin-production, to this mode of generation, and in the very able and ingenious Essay under that title, published in 1849, containing the substance of two lectures, introductory to a most instructive course of lectures on the Generation and Development of the Invertebrated Animals, and also in various parts of these lectures†, has communicated a more lengthened exposition of his views. "The progeny of the impregnated germ-cell," says he, "form the tissues, &c., but not all of them are so employed, some of the derivative germ-cells may remain unchanged, and become included in that body which has been composed of their metamorphosed and diversely combined or confluent brethren: so included, any derivative germ-cell, or the nucleus of such, may commence and repeat the same processes of growth by imbibition, and of propagation by spontaneous fission, as those to which itself owed its origin; followed by metamorphoses and combinations of the germ-masses so produced, which concur to the development of another individual; and this may be, or may not be, like that individual in which the secondary germ-cell or germ-mass was included." ‡ He states farther, that the lower the animal in the scale of life, the number of derivative germ-cells and nuclei which retain their individuality and spermatic power is greater, and the number of those that are metamorphosed into tissues and organs, less. The simplest animals are nothing more than nucleated cells, or in the minute and microscopic ones, as Gregarina and Polygastria, one nucleated cell only; the middle layer of the wall of the Hydra he describes as consisting of nucleated cells. In Compound Polypes and Parenchymatous Entozoa a large quantity of derivative germ-cells is retained among their textures or other parts; and the same is the case at the caudal extremity of the Nais and young Annelida. Professor Owen informs us that he has observed the germs of the viviparous Aphides in the embryoes near the simple digestive sac before any organs have been formed for their reception, and that when these germs are afterwards included in the tubes which correspond to the ovaries and oviducts, he regards them as comparable to the germ-mass in its minutest state of division, and as differing from ova in the absence of the germinal cell.* Notwithstanding the attractive ingenuity of these views, and the great weight which all must be disposed to attach to the statements of so accomplished an anatomist, the theory they involve or expound, when fully considered, does not appear entirely to remove the veil from the mystery of alternate generations, nor to afford that satisfactory explanation or generalisation of its nature which might be desired : for it is to be feared that under the appellation of nucleated cells, as applied to the structure of the lowest animals, very various kinds of organised structures have been confounded by authors, and we are certainly very far from having had determined, by actual observation, the nature or source of the minutely granular masses from which what has been called internal gemmation proceeds; and though it may be admitted that most new structures take their origin in masses of blastema, more or less cellular and granular, the relation of these to the germ-masses of the ovum are far from being ascertained. It may be granted, that in the case of the first brood of Aphides formed in the non-sexual way from the first individual immediately developed in the ovum, a residuum of germ-cells may have served as as the original blastema of their germs ; but when we consider the inconceivably minute portions of this that are to pass to the next and to the successive generations up to nine or eleven, we seem to have to deal rather with a theory of the original pre-existence and "encasement of germs" than with a matter that we can ever hope to decide by observation : and in the greater number of the other instances of alternate generation, there is no possibility of tracing the origin of the germs of the new individuals formed by gemmation to the yolk or germ-mass, of which they are regarded as the included remains.

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* On Alternate Generations, p. 112.

* See Lectures on the Comparative Anatomy of the Invertebrated Animals, 1843, p. 234. and 366.

† As published in the Medical Times, vols. xix. and xx.

‡ On Parthenogenesis, p. 5.

Professor Owen has well remarked †, that "in the Vertebrated, and in the higher Invertebrated animals, only a single individual is propagated from each impregnated ovum. Organised beings might be divided into those in which the ovum is uniparous, and those in which it is multiparous. This is the first and widest or most general distinction which we have to consider in regard to generation, and in proportion as we may recognise its cause will be our insight into the true condition on which Parthenogenesis depends." But this distinction, notwithstanding its acknowledged importance, does not carry us any farther into the insight of the essential conditions of the phenomena by the theory of the residual germ-mass originating new germs; for when the greater part of this mass is converted into the textures and organs of the embryo directly developed from the ovum, there is still as great a difficulty as ever to understand what circumstances should determine a minute residuum, supposing it to exist, to form an entire new individual, or a prodigious multitude of individuals, in place of only an additional portion of texture or an additional organ, which might more naturally be regarded as the correlative products of their brethren germ-cells ; or why, in other numerous instances, in which, to all appearance, an equal quantity of residual germ-mass exists, no such formation of new individuals occurs.

It appears equally fair to suppose that the germs of the ova of all animals must have originated within the ovaries of the female parents from residual germ-cells included in the blastema of these organs; but no distinction has ever been established between that blastema in its primitive state and that of other organs of the body : and there does not appear to be better reason for considering the germs of individuals formed by gemmation, as derived more directly from residual and included germ-cells, than those of the ovarian ova.

I have not adopted the term Parthenogenesis, as applied to the alternate generations, because it implies that this kind of production occurs in female animals. Now, although the observations of Owen and V. Siebold have shown a remarkable similarity to the female structure in the case of the viviparous Aphides, this is altogether wanting in the other instances of alternate generations; and this process is strictly non-sexual rather than uni-sexual in its nature. Were it desirable to change the name for this process, the term "Metagenesis," suggested and sometimes employed by Professor Owen, seems well adapted to express exactly what occurs in alternate generations, without calling for the admission of any hypothesis beyond that of the new production being an act of generation ; and it seems to me to be the most exact translation in scientific terminology that can be given of the German of Steenstrup in "Generations-Wechsel." In a convenient shape it is precisely descriptive of that change of form by generation, or by production of a new individual, which it has been my object to show has been accurately distinguished in the general law of Steenstrup, as different from a mere change of form by growth or by metamorphosis in the same individual.

At the same time it is deserving of notice, that, among the compound Polypina, the continuous multiplication of individuals proceeds to such an extent, and with such remarkable regularity, as to give rise to composite masses, often of very large size, the general arrangement of which bears a considerable resemblance to that of plants : and we are led still more to institute a comparison between these animals and plants by the circumstance of the similarity of their continuous growth by the addition of new sets of polype individuals to the extension of the leaves and branches of a tree or ramified plant, and by the correspondence of the occasional formation of sexual individuals on the polype stock with the development of flowers. It is not without considerable interest, that the same conditions as to temperature, season, supply of nourishment, &c. seem to determine the one or the other kind of production in both the animal and the vegetable bodies. Many botanists regard the plant as an assemblage of individuals ; and zoologists are for the most part agreed as to the distinct individuality of the parts united in a compound polype. But the tendency to spontaneous separation of these individuals, especially in their sexual form, is very frequently exhibited in the animal kingdom, while it is rarely, if ever, met with among plants ; and among the polype tribes, as well as in other examples of alternate generation, the striking difference of form, structure, mode of life, and functions, of some of the sexual individuals developed by non-sexual generation, seem to warn us against extending the comparison farther than the admission of the general analogy above adverted to, or, at all events, precludes us in the mean time from drawing any arguments as to the nature of animal production from that which is as yet only imperfectly understood in the vegetable kingdom.*

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* On Parthenogenesis, p. 38.

† Loc. cit. p. 62.

These considerations raise another question on which recent writers are at issue in regard to the theory of Alternate Generations, viz. whether the various animal bodies formed by the non-sexual process within one act of sexual generation are to be regarded as so many *individuals* composing the species, or whether they are to be considered only as the different states of one and the same individual. I have abstained from entering directly on the discussion of this question, from the desire to avoid the confusion which is apt to arise in it from the use of terms in other than their usual significations. In regard to connected animal forms, such as those which coexist in a Compound Polype, less difficulty might be felt than in those instances in which a complete separation of the progeny from its producer has taken place ; but it seems to require a greater departure from the ordinary signification of a common term than is warranted by our present imperfect knowledge of the phenomena, arbitrarily to determine to regard as merely one individual all those bodies which may be formed by a non-sexual process from the product of a single ovum, notwithstanding the great variations in their structure and mode of life, and the complete separation and apparent independence to which they may attain. It is unquestionably important to acknowledge the integrity and permanence of the species as maintained in the midst of all these variations by generation from an ovum; but there does not seem to be any obvious impropriety in the instances in question in regarding the species as made up of individuals differently constituted among themselves, and produced one out of another by a non-sexual process. The term Zöoid suggested by Huxley, or Zöonite previously employed by Milne Edwards and some other French authors, or any such term agreed upon as implying a relation of affinity among the various bodies included in one act of true sexual generation, may perhaps remove some of the ambiguity ; but I confess I do not think the present state of the inquiry warrants the total abnegation of individuality to the various animal bodies produced in the non-sexual manner.*

In reviewing, then, the whole subject of Alternate Generation, it seems to be equally premature to refer the whole of the phenomena included under this term, which may hereafter be discovered to be very various in their nature, to a simple process of gemmation or individual development, or to attribute them to the existence of certain powers, such as a germ-force or spermatic power, remaining in certain germ-cells, or to reject altogether the hypothesis of Steenstrup of Alternate Generations, which indeed is little more than the expression of the course of the observed phenomena ; until we shall know more exactly the minute structure of the germ from which a bud arises, and the difference between that and the germ of an ovum, and until we shall be more fully acquainted with the whole structure and series of changes of the various animal forms that have been the subject of consideration in the preceding section.

We regard it, therefore, as more consistent with the actual state of our knowledge of the facts to describe the phenomena of Alternate Generation as a peculiar mode of existence belonging to some of the simplest kinds of various classes of Invertebrated animals, which seems to have especial reference to the preparation of the sexual organs; and of this nature, that the animal immediately developed from the fecundated ovum does not usually arrive at sexual completeness, but has formed from it, by a non-sexual process of production, another individual of a different form, or a succession of them, which finally attain to sexual completeness, and produce the fecundated ova that originate the generative cycle; and the effect of which is, to render two or more successive generations of dissimilar animals necessary to the completion of the species to which they belong.

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* For farther remarks on this subject the reader is referred to an account of vegetable production, under the article VEGETABLE OVUM.

* Some acute and interesting remarks by Mr. Huxley on this subject will be found appended to a sketch of J. Müller's discoveries on the Echinodermata, in the Annals of Natural History, 1851, vol. vii. p. 1. I would also refer at this place to the Lectures of M. Agassiz on Comparative Embryology, Boston, 1849, as presenting a most engaging view of the influence which the study of the metamorphosis of animals, along with the history of alternate generations, must exercise on the systematic views in Zoology and Comparative Anatomy; and I also take this opportunity of referring to some remarks by Mr. C. Spencer Bates in a paper on the Development of the Cirripedia, in the Ann. and Mag. of Nat. Hist. for 1851, vol. viii. p. 331., for a statement of the relations subsisting between the various forms of animals considered in their sedentary and free states, either in individual species or in different genera or families of the various classes of animals.

Additional Remarks. — Since the foregoing observations on alternate generation were printed in August, 1852, the knowledge of these peculiar phenomena and of the whole forms of reproduction in various classes of animals has been considerably augmented by several important contributions. A short reference to some of these researches seems necessary in this place, in order to complete our notice of the phenomena referred to.

The statements of Stein, referred to at p. 7. of this article, as to the encysted condition of the Vorticellæ previous to their undergoing multiplication, having been called in question by Ehrenberg,[*], the subject has been farther investigated by F. Cohn, with the result both of a full confirmation of Stein's statements, and of its being ascertained that a considerable number of other infusoria are subject to a similar change; among which he mentions species belonging to the genera Euglena, Prorodon, Chilodon, Notophyra, Trachelius, Trachelocera, and Stentor.[†] Stein holds it to be fully established that the nucleus of the Vorticella is its true reproductive organ. From this nucleus a progeny is formed in two modes, in both of which the parent animal becomes encysted. In one mode the encysted Vorticella is converted into an Acineta-form by the prolongation of narrow contractile processes of its substance from the external surface, and from the nucleus of this Acineta-like animal successive single ones are produced by gemmation. In the other form, the nucleus of the encysted Vorticella undergoing subdivision, becomes converted into the germs or spores of numerous new Vorticellæ. This process is probably in these Protozoa the equivalent of a sexual production of ova; and appears to correspond nearly with that which takes place in the production of the Navicella-like progeny from Gregarinæ, with this difference, that in the latter case two Gregarinæ are united or fused together into a sphere previous to the production of the new progeny of spores.

The view of Leydig, therefore [‡], that the parasitic infusoria named Gregarinæ are only an imperfect or metamorphosed condition of a Filaria, does not appear to be confirmed.

In reference to the Entozoa, recent experiments have furnished ample confirmation of the views now adopted by almost all physiologists, that these animals are the product of a true sexual generation, and that their ova, or embryoes, or larvæ, are introduced from without into the bodies of those animals which they parasitically inhabit; while at the same time the knowledge of their migrations and remarkable transformations becomes more and more precise from additional and renewed investigation of their different forms.

Herbst, who had previously failed in some experiments to cause the transmission of the Trichinæ of the muscles by implantation in wounds of animals, at last succeeded in 1850–51 in causing the muscles of several young dogs to be infected with these parasites by giving them to eat the flesh of a badger which had lived with him for some time in confinement, and in which the Trichinæ existed in great quantity.[*] About the same time Kuchenmeister found that by causing young dogs to swallow along with their food a quantity of the Cysticercus pisiformis (of the hare and rabbit), the intestines of these animals were in a few weeks invariably occupied by a Tænia (T. serrata). Von Siebold, who, as has before been remarked, was the first to advance the opinion (in 1844), that the Cysticercus fasciolaris inhabiting the liver of the rat and mouse is only the early condition of the Tænia crassicolis of the intestine of the cat, has with the assistance of Lewald performed a series of experiments of a nature similar to those of Kuchenmeister, which have established beyond doubt that various kinds of Cysticerci, and also the Cænurus of the sheep's brain, and the Echinococcus veterinorum, are always converted into Tæniæ or Cestoid Worms within a short time after they have been transferred, as by feeding, into the alimentary canal of suitable animals. These experiments have also afforded to V. Siebold the means of observing in a most interesting manner the process of development and gradual conversion of the cystic into the cestoid entozoon.[†]

Since the publication of V. Siebold's experiments, farther researches on the same subject have been laid before the Academy of Sciences of Paris by Van Beneden and by Kuchenmeister, in Memoirs presented by them in competition for the grand prize offered by the Academy in 1853 for the scientific investigation of the Development and Transmission of Intestinal Worms.[‡]

The observations and experiments communicated by Van Beneden in this prize essay, and those contained in his highly interesting Memoir on the Cestoid Entozoa, published in the Mémoires de l'Académie Royale de Belgique for 1850, have also established in the most satisfactory manner the relation between the encysted or scolex condition and the cestoid form of the Tetrarhynchi; facts which have also been in part confirmed by R. Wagner.[§] Van Beneden has observed the first development of the ova of the Tænia dispar of the Rana temporaria[||] into the small embryo provided with its three pairs of boring hooklets, and has watched with care the active motions of these instruments, by which the minute embryoes, scarcely larger than the blood-discs of the frog, penetrate into the tissues or organs in which they afterwards become encysted ; thus affording the most direct proof from observation of the manner in which the young of these parasites become established in the internal parts of animals. The head, with the circle of hooklets and the four suckers, is then formed at the anterior part of the embryo, constituting now the scolex of Van Beneden ; and this author proposes to give the name of proscolex to the previous embryonic stage. In connection with the formation of the head of the encysted animal, it may also be noticed that Stein has observed the three pairs of embryo hooklets remaining for a time irregularly scattered over the enlarged vesicular part of the body.* When the encysted animal (Cysticercus) has been introduced into the stomach and intestine of a suitable animal, generally a carnivorous one, it resists the digestive action of these organs, but speedily loses its caudal vesicle, and gradually acquires the new joints which are formed from the head. It is thus brought to the condition of the strobila, if we choose to liken the jointed state of the tape-worm to the multiple or divided polype stock from which medusæ are thrown off ; and lastly, as the sexual organs become fully developed in each of these joints, beginning in the posterior ones, which are first formed, these are detached one by one, and constitute in the separate condition the bodies named proglottis by Dujardin and Van Beneden. The latter author regards these as alone the perfect animals of the Cestoid, the jointed strobila being only a preparing stock ; and he adheres to the view, previously referred to in this article, that each proglottis approaches in some degree to the organisation of a Trematode animal. According to the views of Van Beneden, therefore, the different stages of a Cestoid worm are the following : — 1st, the ovum ; 2nd, the first embryo or proscolex ; 3rd, the cysticercus, or encysted vesicular body, or scolex ; 4th, the jointed stock, tape-worm, or strobila ; and 5th, the separate sexual individuals, or proglottides.

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[*] Bericht of Berlin Acad. for 1851.

[†] Zeitsch. für Wissen. Zool., vol. iv. p. 253.

[‡] On Psorospermia and Gregarinæ, in Müller's Archiv. for 1851, translated in Quart. Journ. of Micro. Science.

[*] Ann. des Sc. Nat., 1852, tom. xvii. p. 63., and in Quart. Journ. of Micro. Science, No. 3. p. 209.

[†] Zeitsch. für Wissen. Zool., vol. iv. pp. 400. 409. See particularly Plate xvi. A. Also in Annal. des Sciences Nat., 1852, and L'Institut., No. 974.

[‡] See the Report of the Commissioners, by Quatrefages, in Comptes Rendus for Jan. 30th, 1854, p. 166.

[§] See extract of a letter in Ann. des Sc. Nat. for 1853, vol. xix. p. 179.

[||] Comptes Rendus, 1853, p. 788., and in Annals of Nat. Hist., vol. xiii. p. 157.

Among the Trematode animals the production of a successiom of new progenies by a process of internal non-sexual generation has received full confirmation. Van Beneden has added the important fact, however, that some of the Trematoda are not subject to any process of alternate generation or metagenesis. He has traced the whole process of direct development of the animal from the ovum of Udonella caligorum, a viviparous Trematode with large ova. The alternating generation belongs, according to him, to the Oviparous Trematoda, in which the ova are of small size.

In reference to the Compound Medusoid Animals, Siphonophora and Physsophorida, it appears from the researches of Leuckart, Kölliker, Gegenbaur and others *, that the several joints of the connected chains of these animals, as previously conjectured by Milne Edwards and others, may fairly be regarded as distinct, though imperfect individuals, some of which are destined for the sexual production of ova, while the free or floating polypine stock remains destitute of sexual organs. The free polypine stock is first developed from the fecundated ovum, and acquires its one or two swimming vesicles : from it there is afterwards formed the long chain of smaller bodies connected together by an extension of the digestive cavity and external substance of the animal. Some of these form swimming bells or vesicles with prehensile and stinging filaments ; others are digesting cavities or stomachs, and others, most frequently those last formed in the chain, contain one or other of the sexual products, either male and female among the individuals of the same stock, or distinct sexes on separate stocks. But there is sometimes a combination of the motor and nutritive with the reproductive organs in the same individuals of the chain, which warrants fully their being regarded as something more than the mere repetition of organs belonging to one animal. They are, in fact, the same as the sexual individuals of a compound polype ; and in some rare instances, indeed, they have been observed to become detached and to swim about in the separate condition.

In connection with the alternating generation of the Salpæ, in the discovery of which the whole series of facts now under review may be said to have originated, some doubts were in the previous part of the article stated to prevail as to the relation of the sexes in the animals of the aggregated chain. These doubts have now been in a great measure removed, and the knowledge of the whole phenomena of the reproductive processes in these remarkable animals greatly extended by the researches of C. Vogt † and of H. Müller. ‡ From these researches it appears that while, as was previously known, the Solitary Salpæ are entirely non-sexual, the animals united together in the aggregated chain, formed by successive gemmations from one spot of each solitary individual, are hermaphrodite, or possess both male and female sexual products. The ova, however, according to Vogt, are developed at a much earlier period than the spermatic substance : indeed, they are advanced to the condition in which they are ready for fecundation, while their producers are still attached as a chain to their solitary gemmiparous parent. The spermigerous organs only advance to perfection after separation ; and the process of fecundation must therefore be effected in the animals of the attached chain by the spermatic matter derived from detached chains which are frequently floating near them. To this result, no doubt, the currents of water in the respiratory cavity will materially contribute.

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* In observations made on encysted non-sexual round worms, and the encysted condition of a cestoid inhabiting the Tenebrio molitor, and its larva, in Zeitsch. für Wissen. Zool., vol. iv. p. 206.

* Zeitsch. für Wissen. Zool., vol. iv. p. 304., and vol. v. p. 285, &c. ; and Kölliker's Memoir on the Siphonophora of Messina. Leipzig, 1853.

† Bilder aus dem Thierleben, 1852, p. 59.

‡ Zeitsch. für Wissen. Zool., 1853, p. 329.

Since the publication of the first part of this article, the general aspect also of the questions involved in the facts referred to has undergone revision by several authors. The whole doctrine of alternate generation has, it appears, been called in question by Reichert, in a programme entitled Unisexual Reproduction*, which I have not had an opportunity of seeing. In his recent very able and instructive treatise on Reproduction in the Handwörterbuch der Physiologie, Rud. Leuckart†, though he retains the name of alternate generation as designating the phenomena referred to, gives the doctrine little place, and seems still inclined to regard this mode of production rather as a peculiar modification of growth than as a true generation. He is perhaps right in his remark‡, that physiologists have been too much disposed to separate the phenomena of alternate generation from other forms of production of a non-sexual kind, of which he considers them as only a variety; the alternation of different forms being, according to him, only a subordinate and not an essential phenomenon. In his recent very interesting work on Animal Morphology, Victor Carus§ has allowed more importance to the views of Steenstrup, adopting at the same time Owen's term Metagenesis, as most suitable for the designation of this kind of production. This author appears to me to have made the nearest approach to a correct appreciation of the nature of this process in its relation to the whole phenomena of animal reproduction as at present known.

Reviewing therefore finally the whole of the facts and opinions on this subject, I am inclined to adhere to the views expressed in a previous part of this article, that the phenomena of alternate generation or metagenesis ought to be grouped together, and to retain their place as constituting one of the general forms of reproduction among animals; consisting, as they constantly do in a certain number of animals, in the combination, alternation, or succession of the sexual and non-sexual production of individuals all proceeding originally from the development of one ovum. At the same time it is to be noted, that this mode of production does not exist in all the species or genera of those tribes of the lower animals among which it has been observed to occur, and that in some it passes by gradual transitions into other forms of the generative process. It is not on that account the same as them. Metamorphosis and Metagenesis, also, as V. Carus remarks, may be combined, but they are different. "Larvæ, the subjects of metamorphosis, arrive at the state of perfection by throwing off provisional structures which belong to their larval condition, but nurses, the subjects of metagenesis, are themselves entirely provisional structures."

Generation, therefore, or the production of new individuals belonging to a species, may be either of the sexual or of the non-sexual kind. It is only in the Protozoa that the distinction of sex has not yet been discovered. In all other animals the production of new individuals of the species is the result of the development of ova fecundated by spermatic matter. In all the Vertebrate animals and in the majority of the Invertebrate, the development of the ovum gives rise to a single new individual; in most of them by a continuous process of formative growth, in some by successive stages, or by metamorphosis. In a few Invertebrate animals the development of the ovum gives rise directly to more than one individual by what may be named primary division of the ovum. In a considerable number of Invertebrate animals the production of new individuals sexually perfect is not immediate from the fecundated ovum, but secondary or intermediate by non-sexual formation from a preparing stock which is the product of development from the ovum. In such animals an alternation of sexual and non-sexual formation of individuals is necessary for the completion of the act of generation or the reproduction of the species. In a few of these animals only one new individual is formed; but in by far the greater number the product is multiple, thus leading to a great increase in the number of individuals, either in the distinct or in the aggregate form, which have all derived their origin from a single ovum. It is to be observed, however, that in some instances the alternating generation may co-exist either with the non-sexual mode of multiplication or with direct sexual reproduction.

In conformity with these views of the relation of the product of generation to the ovum and its progenitors, there might thus be established the following modes of reproduction among animals—viz.

I. **Monogenesis**, reproduction without known sexual distinction.

II. **Digenesis**, bisexual reproduction.

III. **Metagenesis**, alternation of sexual and non-sexual reproduction.

In each of these main forms of the reproductive process the following varieties might also be distinguished—viz.

1. With single progeny.
2. With multiple progeny.
3. By consecutive development.
4. By metamorphic or interrupted development.

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* Die Monogene Fortpflanzung. Dorpat, 1852.

† Article *Zeugung*, in the 5th and 6th parts of vol. iv. of Wagner's Handwörterbuch, 1853.

‡ Loc. cit. p. 979.

§ System der Thierischen Morphologie. Leipzig, 1853.

PART SECOND.

OF THE OVUM PREVIOUS TO THE COMMENCEMENT OF FŒTAL DEVELOPMENT.

I. ANATOMICAL STRUCTURE, CHEMICAL COMPOSITION, ORIGIN AND FORMATION OF THE OVUM IN MAN AND ANIMALS.

§ I. Preliminary and General Comparison of the Ova of Animals.

At a time when the analogy and difference in the structure and functions of the ova of various animals were less known than at present, and especially before the discovery of the true mammiferous ovum, the phenomena of development were almost exclusively observed in the eggs of birds; and consequently in the progress of investigations on this subject, and their extension to other animals, the nomenclature of parts of the egg, and the interpretation of the phenomena of development, came naturally to be founded on those which had previously been adopted in the study of the egg of the commom fowl. In more recent times it has been found that the egg of birds presents in some measure exceptional characters, as compared with that of the greater number of animals; and it has thus become apparent that the close limitation of our observations to the class of birds, fruitful as they are universally acknowledged to have been in most important and interesting information on our subject, might tend even to retard in some degree the establishment of the more general laws of typical structure and formative change, which constitute so remarkable a feature of the result of modern embryological researches.

Still, the convenience of being able to obtain the egg of the bird without trouble in all stages of advancement, the familiar knowledge that has so long been possessed of the phenomena of incubation, the proportionally large size of the embryo, the difficulty, on the other hand, of making serial examinations of the ova of mammalia, and, though numerous and important, the comparatively fragmentary nature of the observations in this class, and especially in the human subject, make it desirable that we should not too soon depart from the practice, which has so long prevailed, of making the bird's egg the main foundation of our description of the ovum and formative process in general. But, at the same time, the exceptional structure of the fowl's egg alluded to renders it proper for me to present here, in a connected form, some account of the principal differences among the ova of various animals; so that we may, in some measure, avoid drawing false analogies, or deducing supposed general laws, which may be premature, or may be rendered inadmissible by the existence of ascertained individual peculiarities, or more extensive differences among various classes of animals.

In the commencement of this treatise (p. 3.), the ovum of animals has been described as consisting in general of two sets of parts, of which the one is formed in the ovary of the female, and the other is superadded to the first after it has left the place of its formation. The first, constituting the ovarian ovum (or ovulum of some authors), consists essentially of, 1, the external vesicular covering, or vitelline membrane, 2, the yolk or vitelline substance, and 3, the germinal vesicle, with, 4, its nucleus or macula. As being the most constant in their structure and relations, and the more immediate seat and agents of the formation of the embryo, these parts may be regarded as the essential and most important structures of the egg. The other set of parts, which are subject to great variation in different animals, and are only remotely connected with the formative process, consist chiefly of external coverings of more or less density, either membranous or calcareous, within which often is enclosed some portion of albumen or albuminous fluid along with the ovarian ovum. They serve the purpose, in oviparous animals, of protecting the ovarian egg from the hurtful influences of external agents, and, in rarer instances, of supplying additional nourishment to the embryo; in viviparous animals these parts (as in the chorion of mammalia) serve more important ends, being the more immediate means of establishing that intimate organic connection between the parent and embryo, by which a continual supply of materials for the growth of the latter, is transmitted into its body. From analogy, the outermost covering of the ovum of all animals has generally been termed the chorion.

In thus stating the general structure of the ovum of animals, a certain amount of uniformity, analogy, or correspondence in their several parts has in the meantime been assumed; and the best ascertained facts seemed for long, indeed, to have warranted such an assumption. It will be for after consideration to determine how far the comparison of the several parts of the ova of different animals proves their uniformity of structure and relation. In some instances it may appear difficult or impossible to discover the correspondence; and we must therefore be careful not to be led by the attractive nature of a great generalization, to confound a merely functional or physiological analogy, with an anatomical, a structural and relational identity.

Without entering at présent into a detail of the observations bearing upon the foregoing view of the general analogy in structure and function of the ova of animals (which in truth would involve the history of almost all the more recent researches on the subject), it seems proper at this place to call the attention of the reader to the most prominent modern discoveries which have laid the foundation of a more accurate acquaintance with the structure of the ovum, and have also led to the application of improved histological views of the study to ovology.*

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* It is not intended at this place to refer to the history of discovery in the department of our subject which includes embryological development, in which

The first modern discovery, which introduced a far greater accuracy into the study of ovology than existed previously, was unquestionably that of the germinal vesicle in the ovarian ovum of birds, by Purkinje, of Breslau, in 1825*, an observation which led directly to the ascertainment of the general fact that such a vesicle exists invariably in the ovarian ovum of all animals. The extension of this discovery to a variety of oviparous animals, we may consider as due, in the first instance, to Von Baer and R. Wagner.

The next important discovery in chronological order, which contributed, in an eminent degree, to remove one of the greatest difficulties in our subject, was that made by Von Baer, in 1827, of the minute ovum of mammalia, or true viviparous animals.† The discovery of the nature of the mammiferous ovum was rendered complete in 1834, by the observation of the germinal vesicle first by Coste and somewhat later but independently by T. Wharton Jones ‡ ; and the knowledge of the mammiferous ovum was greatly extended and confirmed by the observations of G. Valentin and Bernardt, of Breslau.§

The nature of the germinal vesicle itself next attracted the attention of ovologists, and a farther addition to the knowledge of its structure was made by Rudolph Wagner, of Göttingen, in 1835, by the discovery in it of a minute particle or mass of fine granules, to which he gave the name of macula germinativa, or germinal spot.* The subsequent researches which that author instituted on the earliest condition of the ovula in the whole series of animals, contributed, more than any others of the same period, to establish the doctrine of a general uniformity in the structure and mode of origin of the ova of animals.† Although it appeared, from the researches of R. Wagner, and has been made still more apparent from late observations, that in several classes of animals the germinal macula loses its determinate form and is subdivided and diffused, as it were, in the germinal vesicle, yet the more circumscribed form of this body, in its earliest condition, and its general prevalence, as a constituent part of the vesicle in almost all animals, seem to indicate the analogy of that vesicle with the true nucleated cell of other parts of the animal body.

After the general nature and structure of the ovum had been ascertained by the several discoveries now mentioned, numerous and important researches followed one another in rapid succession, giving greater extent minuteness, and accuracy to, and in some instances modifying and correcting, the knowledge previously acquired. Among the authors of these researches, besides those already mentioned, the names of Rathke, J. Müller, Prevost and Dumas, Barry, Reichert, Bischoff, Kölliker, and Vogt, occupy the most prominent place. Of these and others, more special mention will be made in the progress of our history of the ovum and its development. But, as my present object is to place before the reader only the principal discoveries which may be regarded as the groundwork of the scientific knowledge of our subject, I will only farther call attention at this place, to the influence which the ob-

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Malpighi, Wolff, Döllinger, Von Baer and Pander took a prominent part, but only that which belongs to the structure of the ovum itself.

* This discovery was first announced in a small work, entitled Symbolæ ad Ovi Historiam ante Incubationem, Auct. Joann. Evang. Purkinje; printed at Leipzig, in 1825, on the occasion of the celebration of Blumenbach's Semisecular Jubilee. A second edition in 4to. with two lithog. plates, appeared in 1830. Purkinje is also the author of the Article *Ei* in the Berliner Encyclopædisches Wörterbuch, in 1834.

† See the Epistola de Ovi Mammalium et Hominis Genesi. Auct. Car. Ern. De Baer, published in 4to., at Leipzig, in 1827; and the interesting Commentary on or Supplement to the same in Heusinger's Journal; and the translation of both of these writings in Breschet's Répertoire d'Anatomie et de Physiologie. 4to. Paris, 1829. As I shall have occasion to return to the history of this discovery, I will not enter on further details here; but it is right to state that Messrs. Prevost and Dumas may in some measure be considered to have shared in the merit of the discovery; as, in an extended and highly illustrative series of experiments, instituted by them as early as 1824, they were led to the conclusion that the ovules of mammiferous animals, of extremely minute size, were really contained in the Graafian follicles previous to conception; and they even appear to have twice seen in the contents of very advanced follicles, a small spherical body which could be no other than the ovule. See Annal. des Scien. Nat. tom. iii., 1824, p. 135. But Von Baer first demonstrated this body with precision, and explained its relations to the follicle, &c.

‡ Coste's discovery of the germinal vesicle in the rabbit, was communicated to the public in the Comptes Rendus for 1833; it is fully described in his Recherches sur la Génération des Mammifères, &c.; 4to. Paris, 1834. In 1835, Thomas Wharton Jones read a paper to the Royal Society of London, containing an account of his observations on this vesicle in the mammiferous ovum, made without a knowledge of those of Coste in the autumn of 1834; but this paper was not printed in the Transactions of that year. It was afterwards published in the Lond. Med. Gazette, in 1838, p. 680. This discovery was confirmed and extended by Valentin and Bernardt, whose observations are recorded by the latter in his work, Symb. ad Ovi Mammal. Hist. ante Prægnationem, Vratislaviæ, 1834.

§ See G. Valentin's Handbuch der Entwickelungsgeschichte des Menschen, &c.; 8vo. Berlin, 1835, at p. 14. The part of this work relating to the structure and formation of the ovum, was translated and published by Dr. M. Barry, in the Edin. Med. and Surg. Journal, No. 127.

* The observations of R. Wagner on this subject, were made towards the end of 1834. This discovery was first published in the 1st Edit. of his Lehrbuch der Vergleich. Anat., 8vo., Leipzig, 1834—35, pp. 320 and 352, and in Müller's Archiv. for the latter year, p. 373.

† His more extended researches are described in the work entitled, Prodromus Historiæ Generationis Hominis atque Animalium: folio, Leipzig, 1836. With two copper-plates and very numerous figures. These and the researches of Valentin, are with reference to the ovum, peculiarly interesting and important as the immediate precursors of the Microscopic Researches of Schwann. See also, the Beiträge zur Geschichte der Zeugung and Entwickelung, by R. Wagner; published in the Trans. of the Roy. Bavar. Acad. of Sciences, 4to., Munich, 1837.

R. Wagner is also the author of the Article *Ei* in Ersch and Grüber's Encyclopædie.

servations and doctrines of Schwann, as to the cellular origin and constitution of the textures of plants and animals, published in 1838, have exerted on the progress of ovology and embryology. In accordance with his general views, Schwann regarded the ovarian ovum as constituting an organised cell, of which the vitelline membrane is the outer cell-wall, the yolk substance the contents, the germinal vesicle the nucleus, and the macula or maculæ the nucleolus or nucleoli.* While the observations of Schwann do not present us with any very important new facts as to the structure of the ovum in particular, and although it may be necessary even to modify, in some degree, the view we should now, with our increased knowledge, be disposed to take of its relation to other organised cells of the economy, still it cannot be doubted that the great generalisation matured by this author has exerted, and still continues to exert, upon the progress of discovery and the scientific aspect of our subject, a no less remarkable influence than that which has been apparent since its first promulgation, on almost the whole range of physiological anatomy; furnishing the key to the structure of the ovum itself, laying the foundation of the histological laws of development, bringing a vast amount of observed facts under a consistent doctrine, and stimulating and guiding the embryologist in new paths of research.†

The most important general facts that have been ascertained in regard to the ova of animals may now be stated shortly as follows:—

1. The ova of animals begin to be formed in the ovary of the female parent at an early period of life, and are produced more commonly in vesicular, more rarely in tubular, cavities or ovisacs of these organs.

2. In those instances, in which it has been possible to detect the earliest stages of formation, the ovum appears very generally to take its origin in the form of a minute spherule or vesicle. This soon enlarges, and is converted into a nucleated cell, which forms the germinal vesicle, and this remains as a constituent part of the ovulum, till the latter is about to leave the ovary, or till the first formative changes commence.

3. The vitellus or yolk substance begins to be formed a little later. It is gradually accumulated, either in the vicinity of or round the germinal vesicle, in some rarer instances being produced in a separate organ; it consists of an albuminous fluid in which are suspended a large quantity of granules and oil spherules, or of larger corpuscles, having the form of non-nucleated simple cells. The structure of the yolk substance is subject to considerable variety.

4. The yolk substance and germinal vesicle are together enclosed, in the mature state of the ovarian ovum, by an almost structureless vesicular vitelline membrane, which in most animals is formed later than the other parts, in some at an early period in others comparatively late, and which is not, therefore, to be invariably regarded as a true cell-wall, or as an original part of the ovum.

5. The germinal vesicle presents several of the characteristics of a true organised cell: the macula, or germinal spot, has in many animals the form and relation of a nucleus; but in some, the subdivided structure of this macula, which succeeds in the progress of formation of the ovum, causes it to lose its simple nuclear object.

6. When the ovulum, or ovarian ovum, attains maturity, it generally leaves the place of its formation in the ovary, and about the same time—in some animals before, in others after it—the germinal vesicle disappears, bursts, or dissolves. In the greater number of ani-

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* Schwann, after hesitating somewhat whether to regard the entire ovum or the germinal vesicle as a true cell, gave the preference to the above view, chiefly from a consideration of the manner in which the ovum was believed to be formed, and its correspondence, as he conceived, with the invariable and necessary mode of formation of cells in general. These latter views have themselves undergone some modification since the publication of Schwann's Researches, and we shall probably find (as will afterwards be more fully stated) that a study of the structure and mode of production of the ova in a variety of animals, may render it necessary to modify also the comparison of the parts of the ovum to the organic cell, adopting rather the view of R. Wagner and Henle, according to which the germinal vesicle is regarded as the true cell, and the other parts of the ovum as of the nature of superadded structures.

† Mikroskop. Untersuch. über die Ubereinstimmung in der Struktur und dem Wachsthum der Thiere und Pflanzen, von Dr. Thomas Schwann. Berlin, 1839. The interesting researches of M. J. Schleiden, on the cellular structure of Plants, entitled Beiträge zur Phytogenesis, published in Müller's Archiv. for 1838, immediately preceded those of Schwann; and they may be considered as forming in some measure, along with his, the basis of modern histology: the researches of the latter author were independently made, and an extract of them published in the beginning of 1838, in Froriep's Notizen: and the two first parts of his fuller treatise were sent to the French Academy in August and December of 1838. An interesting analysis of both these works in the British and Foreign Medical Review, vol. ix. for 1840, made their contents generally known in this country; and an excellent translation of them both by Mr. H. Smith has since been published (1847) under the auspices of the Sydenham Society. It may be observed, however, that the great and important generalisations which Schleiden and Schwann have, with so much merit, established, may in some measure be regarded as the fulfilment or amplification of, and true deduction from, a variety of detached observations, which had been accumulating, in regard to both kingdoms of nature, for some years, more especially after the improvement of the achromatic microscope had given increased facility and precision to the minute examination of the tissues; such as the discovery of the nucleus of the vegetable cell by Robert Brown in 1831; the discovery of the cellular structure of the chorda dorsalis by J. Müller; the observations of Henle on epithelium, of Valentin on several similar subjects, and of Turpin and Mirbel on plants, together with the observations previously referred to on the ovum of animals itself. But these detached observations had not led to any important general views before the publication of the Researches of Schleiden and Schwann.

mals, it is uncertain what becomes of its substance.

7. In the greater number of animals the ovum acquires some additional parts, such as albumen, external coverings (shell, chorion &c.), in its descent through the passages of the female parent after leaving the ovary; in some animals an external covering corresponding with the chorion is already formed in the ovary.

8. When the spermatic substance of the male parent has come in contact with the ovum, so as to exert its peculiar fecundating influence upon its germinal part — an action which in a few animals occur before, but in the greater number shortly after it has left the ovary — the first of the series of changes which follows, and is preparatory to laying the foundation of the new being, consists, in almost all animals, in a peculiar process of division, cleavage, or segmentation, which affects either the whole yolk, or a part of it, or that portion only in the vicinity of which the germinal vesicle has before been situated and in which the rudiments of the embryo afterwards make their appearance. This subdivision proceeds continuously, till the whole germinal part of the yolk is reduced by it to a nearly uniform mass of corpuscles, or structural elements of microscopic size, which generally occupy or are spread over more or less of the surface of the yolk mass within the vitelline membrane.

9. The rudiments of the embryo, and its accompanying organised structures in the ovum, when such exist, are first formed in the centre of a layer of nucleated organised cells, named by Pander *Blastoderm* or germinal membrane, the formation of which results more or less directly from the process of segmentation above referred to. The disappearance of the germinal vesicle when the ovarian ovum arrives at maturity, the influence of fecundation acting about the same time, the process of yolk-segmentation which immediately follows the latter change, and only occurs as a consequence of fecundation, and the formation of the germinal membrane or blastodermic layer of cells, in which the segmentation results, are successive phenomena of change in a fruitful ovum, which undoubtedly stand in some very immediate and close relation to each other; but the exact nature of that relation is still involved in some degree of obscurity. In some animals the process of yolk-segmentation seems either in itself to be a process of rapid cell-formation, or to be accompanied by it; while in other animals (chiefly those highest in the scale), the segmentation is only the immediate prelude to the generation of the true nucleated cells, which afterwards constitute the blastoderm.

10. The centre of fœtal development is coincident with the place of the germinal vesicle in the mature egg, and with the centre of the blastodermic layer of cells; and it would appear, also, that the principal axis of the embryo is coincident with the line of first division of the germinal part of the yolk in the commencement of segmentation: but it is yet undecided what part the germinal vesicle or its nucleus or macula more immediately take in the segmenting process, or in the origination of the true embryo-cells; and in the higher animals, at least, it is still uncertain whether or not these embryo-cells are the direct progeny or descendants of the germinal vesicle or its nucleus. The germ spot, the centre of the first segmentation, and the centre of embryonic formation, constitute, therefore, a constant point in all animals, which may be termed the germinal centre of the ovum.

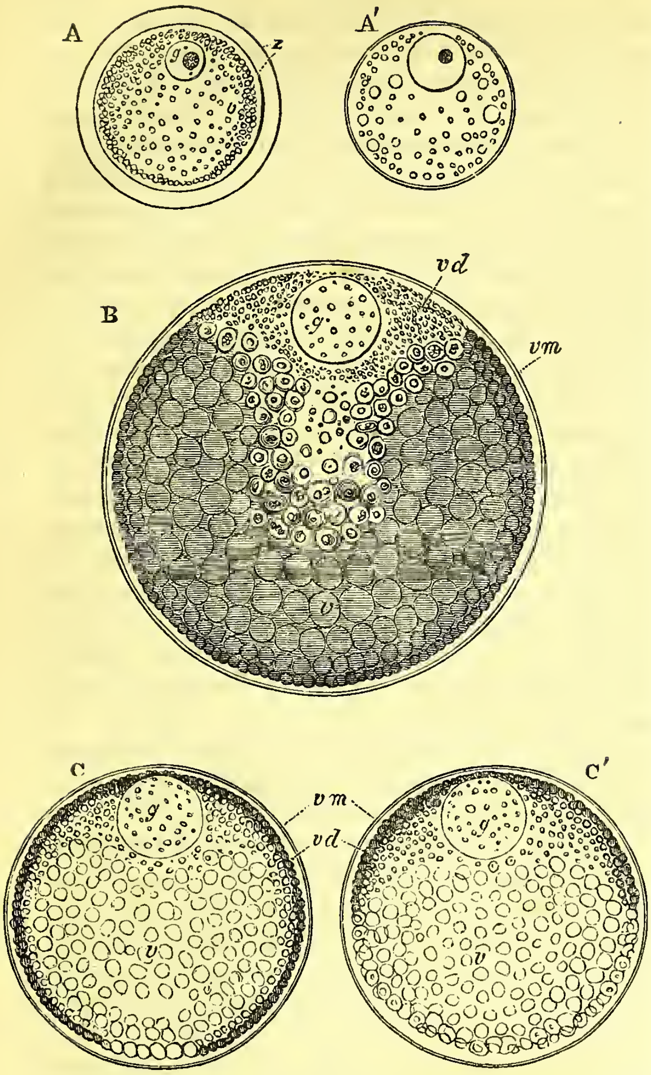
Division of the Ova of Animals into Groups. — Although the researches of modern ovologists thus enable us to assert with confidence the general similarity of structure in the ova of animals, and to point out general features of correspondence in the phenomena which they exhibit in their first origin, progress to perfection, and conversion into the rudiments of the new being; yet it must be admitted that very important differences are also to be observed among various ova, more especially when they have reached a state of maturity. In what has previously been affirmed, therefore, of the similarity of animal ova, it is to be understood that uniformity of a general kind only is implied; and even that correspondence is demonstrated not so immediately, in many instances, by the examination of the fully formed ova, as by their careful comparison, at different stages of their growth, and more especially in their earlier conditions.

The more important of these differences are those which are related to the nature of the germinal portion of the ovum, as compared with the rest of its parts; and a consideration of these differences, in so far as they have yet been observed, appears to lead to a division of the ova of animals into three principal groups, as follows: —

First group. — In a certain number of animals, some of which are viviparous, others oviparous, the ovum is for the most part of proportionally small size, sometimes very minute, as compared with the full-grown parents, and of very simple structure; the yolk substance is entirely composed of elementary granules, or minute and simple spherules; the process of segmentation affects the whole mass of the yolk, and the germinal or blastodermic layer, resulting from that segmentation extends from the first over the whole surface of the ovum; the whole of this layer contributes at once to the formation of the rudiments of the embryo and its accompanying organised structures; the whole yolk, or ovulum, in fact, is germinal, or is converted into the parts of the future embryo. Such is the nature of the ovum in mammalia, and among the Invertebrata, in most Mollusca, Entozoa, Echinodermata, Acalephæ, Polypes, and a considerable number of other tribes.

Second group. — In another set of animals, the great majority of which are oviparous, the ova are proportionally of the largest size; the yolk substance consists very obviously of

Fig. 31.



Diagrammatic representation of the three principal kinds of ovarian ova, in sections (the relation of size not, however, being maintained).

A. Mammiferous ovarian ovum; *z.* zona pellucida or vitelline membrane of some authors; *v.* granular yolk substance; *g.* germinal vesicle, with its nucleus or germinal spot; A′. young ovum of a molluscous animal.

B. Young ovarian ovum of a bird; *v. m.* vitelline membrane; *v.* large yolk corpuscles of two kinds—viz. those of the yellow external part, and those of the cavity; *g.* germinal vesicle without spot or nucleus, but granular diffused maculæ; *v. d.* small granular yolk substance forming the vitelline disc.

C. Ovarian ovum of a batrachian reptile; *v. m.* vitelline membrane; *v. d.* vitelline disc, or formative yolk substance deeply coloured, and surrounding the large granular yolk substance, in one nearly entirely, in the other, C′, only half round the ovum; *g.* germinal vesicle.

two kinds of organised particles, — viz., of smaller granules nearly similar to those which form the whole yolk in the last group, and of larger cells, usually non-nucleated, and fat vesicles, which constitute the greater part of the mass. The first or granular part of the yolk constitutes a thin disc, limited to one region of the surface, — viz., the upper side in the vicinity of the place occupied by the germinal vesicle, while the cellular substance of the yolk forms the larger spherical mass of the egg. Besides these two, there are also various intermediate forms, which seem to be stages of transition between the other kinds of structural elements. The germinal vesicle in the ripe ovarian ovulum, is situated in the centre of the granular disc, and after its disappearance, the process of segmentation is limited to that disc. The germinal or blastodermic membrane, or layer of cells, extends, therefore, at first, no farther than this granular disc, and consequently it is only a very small part of the ovum which directly contributes to lay the first foundations of the embryo, or its accessory parts; while the larger mass of cellular yolk comes only secondarily to take a part in the process of embryo nourishment. Hence, in such ova, the distinction may be broadly drawn between the germinal or formative, and the nutritive parts of the yolk. Such is the invariable relation of the parts of the ovum to development in the whole class of birds, with some differences in scaly reptiles, in cartilaginous fishes, and perhaps also in cephalopodous mollusca, and a few other invertebrata.

Third group.—In another group of animals the structure and relations of the parts of the ovum are different from, but in some degree also intermediate between, those of the two groups previously described. In this one the yolk, or ovulum, may be stated to be of middle size; its structural elements appear to be of two kinds,—viz., the smaller germinal or formative granules, and the larger, or nutritive corpuscles; but these last are in less quantity, are subject to considerable variety, and exhibit less of the cellular structure which characterises the ova of the previous group. The germinal layer occupies a larger portion of the surface of the yolk than in the large-yoked ova (second group), but in general less than in the small-yoked ova (first group), and its extent is subject to considerable variety; in some, covering not more than a half, in others extending nearly over the whole surface of the yolk. The segmentation is co-extensive with the germinal part, and more or less of the yolk, therefore, contributes at the first to form the primitive parts of the embryo. Such is the condition of the ovum in the Scaleless Reptiles or Amphibia, and Osseous Fishes. The ova of the higher crustacea, Arachnida, Insecta, and some other Invertebrata may perhaps be included in the same group.

It will be perceived that in the three groups now mentioned, a distinction has been drawn between a part of the yolk, which is immediately employed in the formation of the embryo, and another, which is only remotely connected with that process. In the bird's egg, it has been stated that the latter part of the yolk is in large quantity, and that in the minute mammiferous ovum the first part only exists, and that in batrachia the two kinds of yolk substance are more nearly equally balanced. This difference among the ova of animals has been long known to physiologists in a general way; but its true nature, as connected with a difference of structure of the two kinds of yolk substance, and their relation to the earliest development of the embryo, has of late attracted considerable attention, and appears to have been first clearly stated by Reichert in 1840, and afterwards in 1843 *; and in accordance with the views of that author, we may with propriety distinguish the formative (or germinal) from the nutritive parts of the yolk. In the fowl's egg, for example (in which it must be admitted these two parts were long confounded together), the cicatricula, together with its so called nucleus, and a part perhaps of the lighter-coloured substance which occupies the centre of the yolk and the canal extending from it to the cicatricula, constitutes the formative or germinal part ; and the larger mass of the more deeply-coloured portion of the yolk forms the nutritive vitelline substance. In the mammiferous ovum, on the other hand, the latter part is either entirely absent, or is in small quantity, and the whole of the yolk substance may be looked upon as directly formative, or as analogous to that which forms only the cicatricula of the fowl's egg. Among more recent writers, the distinction of these parts has been particularly insisted upon, and illustrated by M. Coste†, and also by Messrs. Prevost and Lebert.‡

The difference in the relative amount of the formative and nutritive yolk substance, as well as in the size of the whole ovum, in birds and mammalia, is manifestly to be regarded as more immediately connected with the different manner in which the embryo is to be supplied with the materials necessary for its growth in the two cases ; in the oviparous mode of development, the whole amount of nourishment required being provided in the egg itself, and detached along with it from the parent ; in the truly viviparous mode, a continual addition of new materials for growth, being made by transmission from the maternal parent in the placenta, or in some analogous structure, which accompanies utero-gestation.

The smaller proportional size of the nutritive part in Batrachia and Osseous Fishes (though most of these animals are truly oviparous), may be attributed to the very early period of development, and consequent small size of the embryo at the time when in these aquatic animals it leaves the egg, and, taking upon itself an independent life, gathers nourishment in the same manner as the adult animal.§

The above arrangement is by no means offered as exhausting the divisions which might be formed of the ova of animals, but rather as bringing forward prominently the most remarkable characteristics of those of vertebrata. It is not improbable that a more accurate acquaintance with the structure of the ova in the animals thus grouped and more especially of the Invertebrata, may lead to some considerable modifications of the divisions here adopted ; but the main distinction upon which they are founded is so important, that even with our present incomplete acquaintance with them, it seems advisable to call attention to it at this place. As I shall have occasion to refer frequently to these groups in the subsequent description of the ova of various animals, in the absence of more appropriate appellations, I will, for the sake of brevity, designate them severally, as follows,—viz., 1st group, *Small-yoked ova*, as in Mammalia ; 2nd group, *Large-yoked ova*, as in Birds, Scaly Reptiles, and Cartilaginous fishes; 3rd group, *Middle-sized yoked ova*, as in Batrachia, Osseous Fishes, &c.

§ 2. Further comparison of the ova of animals in general, as respects their size, number, form, and the relation of their parts.

Size of ova.—In addition to what has been said on this subject in the previous section, it may farther be remarked that, in the second and third groups, the size of the ova of different genera and species is to a certain extent proportional to that of the adult animal, or of the fully-developed fœtus ; but in the first group, or at least in Mammalia, in which the nutritive part of the yolk may be considered as wholly or nearly entirely absent, there is a much greater uniformity in the size of the ova ; and, accordingly, the largest mammiferous animal may take origin from an ovum which, when mature, is even smaller than those of species of animals many hundred times less in bulk ; while in the class of Birds, we observe the nearly regular increase of the size of the ovum in proportion to that of the parent animal, from the smallest humming-bird up to the ostrich, or the still larger egg of the Æpyornis, an extinct bird, of which some of the bones, along with the eggs, have recently been discovered in Madagascar.*

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* Entwickelungsleben im Wirbelthierreich ; 4to. Berlin, 1840 ; and in Beiträge zur Kenntniss des heutigen Entwickelungsgeschichte ; 8vo. Berlin. 1843, p. 22.

† Cours d'Embryogénie Comparée, tom. i. Paris, 1837 ; and Histoire gén. et partic. du Développement de l'Homme et des Animaux, Paris, tom. i. 4to., 1848.

‡ In Annal. des Scien. Nat. for 1844. 3rd. Ser. tom. i. p. 193 and 265.

§ At the same time it is to be kept in mind that there are exceptions to these relations, which make it extremely difficult to state any general law of connection between the structure of the ovum and the mode of gestation and place of development of the embryo ; as in the case of a few of the lizards and serpents, and some cartilaginous fishes, in which although the egg agrees in general structure with that of animals which are generally oviparous, it is retained in the oviduct or uterus of the female during a part or even the whole of the time of fœtal development ; and there are also exceptions in the third group—viz. that of batrachia and osseous fishes as in the Land Salamander and Viviparous Blenny. To this mode of gestation the name of Ovoviviparous has been given. There are many varieties of a similar kind among the Invertebrata, and on the whole it may be stated that there is no constant correspondence between the size of the ovum and the mode of gestation. The Marsupiata also and the Monotremata among the Mammalia, exhibit interesting modifications, in the first a partial, and in the second, probably a complete residence of the ovum in the uterus of the female parent during development ; while the ovum in these animals approaches, in some respects, the type which is more commonly oviparous.

* The circumference of this extraordinary egg

In illustration of the most striking of these differences of size in the ova of animals, the following examples may be referred to: — The human ovum is a body not more than $\frac{1}{200}$ of an inch in diameter; so minute, in fact, that we can scarcely form any estimate of its weight or quantity of matter. Let us assume, what seems probable, that it weighs about $\frac{1}{1000}$ of a grain. Now, if we take the weight of a full-grown fœtus as between six and seven pounds, or 45,000 grains, and the adult human body as about 120 or 130 lbs., or 900,000 grains, it appears that while the full-grown fœtus bears the proportion of one-twentieth of the weight of the adult, the ovum is scarcely a thousand-millionth part. In the fowl, the entire egg, when newly laid, weighs about 2 ounces, or 900 grains, and is nearly one twenty-second part of the weight of the adult body, supposing it to be somewhat under 3 lbs. The chick, produced by incubation, is about 600 grains in weight, or about two-thirds of the egg, and is, therefore, somewhat less than a thirtieth part of the weight of the adult. Again, let us take the weight of an osseous fish (as in a female cyclopterus lumpus recently measured by myself), at 9 lbs. 8 ounces, or 66,500 grains; one of the ova, which were fully developed and filled two enormous ovaries, weighed one-seventh of a grain; and the fœtus of such a fish, when it first leaves the egg, might probably weigh not more than one-tenth of a grain; so that the egg would be in the proportion of 1 to 500,000, as compared with the body of the fish.

It is to be observed, however, that this great disparity of size belongs principally to the nutritive part of the egg, and that there is a nearer approach to uniformity in the size of the germinal vesicle; but in this, too, we shall afterwards see that the size is greatest in the ova of the second group, in which the whole ovum attains the greatest magnitude. In the mammiferous ovum, the germinal vesicle is about $\frac{1}{600}$ or $\frac{1}{800}$ of an inch in diameter; but in the fowl's egg it is of a diameter about ten times greater, and in cartilaginous fishes it is even of a somewhat larger size; but still in no egg does this vesicle depart altogether from that small and almost microscopic magnitude which may be regarded as characteristic of the elementary organic structures.

The size of the ovary, when full of developed ova, is also deserving of notice, as giving some indication of the relative amount of reproductive power in the three groups before distinguished. Thus, in the human species, the two ovaries weigh about 500 grains; in the fowl, when developed at the breeding season, the ovary, with its yolks, may weigh 1,500 grains; and in the lump fish, above mentioned, the ovaries weighed together 3 lbs. and 3 ounces, or 22,300 grains. Thus the ovaries were to the body, in the first, as 1 to 1,800; in the second, as 1 to 13; and in the third, as 1 to 3.*

The following table may serve to exhibit these proportions in a general way: —

Weight in Grains of the —

	Ovum.	Ovaries.	Fœtus.	Adult.
Mammifer -	0·001	500	45,000·0	900,000.
Fowl - -	900·000	1500	600·0	20,000.
Osseous fish -	0·135	22,300	0·1	66,500.

Number of ova.—The number or quantity of the ova which the females of different animals are capable of producing in a given time, or during the whole of their lives, is so various, that only a very vague statement can be made in regard to it. The very great productiveness or fecundity of osseous fishes, and of many of the invertebrata, is well known. The ovary of the herring has been found to contain 25,000 ova. In the Cyclopterus lumpus, before referred to, the number of ova estimated as being contained in the ripe ovaries together was about 155,000; and in the ovaries of a Holibut or Hippoglossus, of 156 lbs. weight, I found about three and a half millions. The queen ant of the African termites is said to lay 80,000 eggs in 24 hours; and the common hair worm, or Gordius, as many as 8,000,000 in less than a day. The Entozoa appear to produce the greatest number of all animals — a fact which is somewhat surprising, when we consider how few of these animals comparatively reach their adult condition. In many of the above animals this enormous production is not a single act, but is repeated again and again in successive seasons.

In birds and those animals belonging to the second group, in which the eggs are proportionally of large size, comparatively few of the ova, of which the germs are visible in the ovaries, come to maturity; and in the natural state only a small number are productive. But it is well known that great variations may be caused in this respect by the condition of the animal; and that in a state of domesticity, and under high feeding, a much greater number of eggs may, in some birds, come to maturity, as in the common fowl, in some kinds of which, indeed, an egg is laid daily for two-thirds of the year — a production which would amount to upwards of 30 lbs. or ten times the weight of the whole animal; and, if

over its long diameter, is stated to have been nearly three feet, and over its short diameter two feet four inches; its greatest length nearly thirteen inches. M. Isidore Geoffroy estimates that it must have contained $10\frac{1}{3}$ quarts of substance, or nearly six times as much as an ostrich's egg, 148 times as much as an ordinary hen's egg, and 50,000 times as much as that of a humming bird. Notwithstanding, however, that in the class of birds there is a general correspondence between the size of the egg and the stature of the adult, this correspondence is not regular or constant, and Prof. Owen has illustrated this fact in a striking manner by reference to the Apteryx of New Zealand, which produces a proportionally very large egg.

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* The Article "Zeugung" by Leuckart, contained in two parts of R. Wagner's Handwörterbuch der Physiologie, and which I have only received since the above was written, may be consulted as containing fuller information on the same and the following subject.

the product of different successive years be taken together, a fowl may, at the most, bring forth about 1,200 eggs. I have attempted to count and estimate the whole number of ovula in the undeveloped state to be seen in the ovary of the common fowl, and I find it to amount to 30,000 or 40,000. A great many of these ovula must, therefore, be unproductive in the higher oviparous animals, their germs either remaining undeveloped or being absorbed in the ovaries.

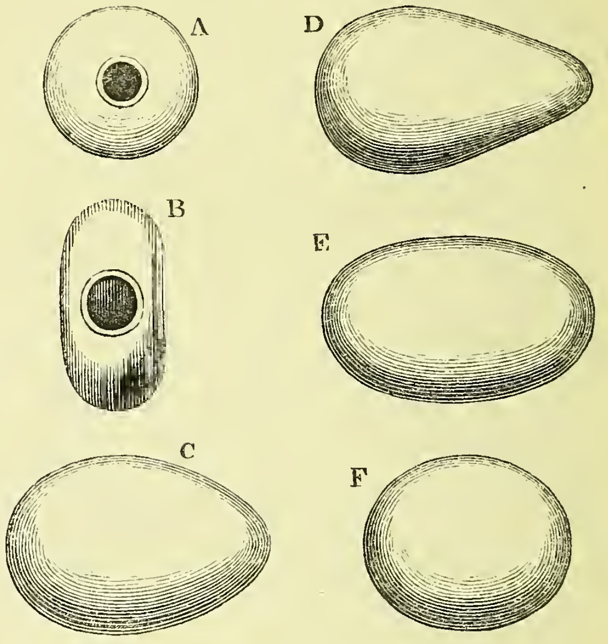
In mammalia, and in the human species, although only a few ovula approach to maturity at a time, and a small number only of the ova, as compared with the whole of those contained in the ovaries, serve for production of the offspring, it is known that a considerable number is discharged from the Graafian vesicles of the ovaries in the unimpregnated state. Thus, in the human female (as will be more fully stated hereafter), one or more ovula are discharged from the ovarian vesicles at every successive four-weekly menstrual period during about 30 years of life, and thus not less than 400 ovula may be excluded from the ovaries; but this number is probably greatly below that of the whole ovula or their germs, which the human ovaries contain; and the ovaries of many quadrupeds present, undoubtedly, a greater number.

External form and relation of the parts.— The ovum, being composed of cellular, granular, and fluid substance, and being enclosed by an entire vesicular membrane, has generally, at least in its early condition, a spherical form. In the mature state, this form is in many instances retained; but there is also not unfrequently a departure from it, in consequence of the addition of the external parts unequally deposited on the surface of the more globular yolk within them. This spherical form of the ovarian ovum points to its isolated mode of production, and its destination for a separate existence, and is characteristic of the elementary nature of its organic structure.

In the class of birds, the egg is always covered in by an external hard calcareous shell; and in the greater number the external form given by this is somewhat elongated, and not unfrequently, as in the common fowl, with a difference of the size and curvatures at the opposite ends, caused by the manner of the descent through the female passages. There are, however, considerable differences among the different families of birds, as in the nearly globular form of the predaceous, the more elongated form with nearly equal ends in some of the ducks, the well-known shape of the gallinæ and others allied to them, and the greater disparity at the opposite ends, as in the seafowl.*

In those of the scaly reptiles which are oviparous, there is also a firm external covering; but only in some of them, as in most chelonia and in the crocodiles, is there a hard calcareous shell. In the greater number of the sauria and ophidia, the external covering is of a tough membranous or parchment-like consistence, formed of several layers of condensed fibro-albuminous substance, in which either no calcareous matter, or only a small quantity of it, is contained. In those serpents and lizards, again, which are ovoviviparous, the egg, when it descends into the oviduct, is not covered there with the firm external envelope, but with a thinner and softer membrane, similar somewhat to the membrane lining the shell in birds.

Fig. 32



External forms of different eggs of Birds and Reptiles.

A. Batrachian reptile, frog or toad; spherical shape, the dark yolk within, the gelatinous albumen externally; swollen by imbibition of water.

B. Triton or Salamander; elongated external membrane, coloured spherical yolk within.

C. Oval of unequal curves at the two ends, as in gallinaceous, passerine, and many other birds.

D. Very unequal size of the two ends, as common among sea-fowl.

E. Equal oval, as among some ducks, the crocodile, lizard, &c.

F. Short oval or nearly spherical, as in predaceous birds, chelonia, &c.

In the oviparous cartilaginous fishes, a peculiar horny capsule is formed round the yolk and albumen, as they pass through the oviduct at a place where a particular gland is provided for its formation. These capsules are of a fibrous structure, of an oblong, somewhat quadrilateral shape, as in the skate and shark, and, at each angle, are prolonged into tubular processes or filaments, of great length in some sharks, which when short and open, may allow of the passage of water to the embryo contained for a long time within the ovum; and serve also the purpose, when long and convoluted, of entangling and attaching the egg capsule among seaweed and floating bodies.

I have found that in the Myxine glutinosa the globular yolk is enclosed in a horny capsule of similar consistence and structure, but of a simple elongated ellypsoidal shape, and in place of four terminal angular tubes, a number of trumpet-shaped tubular processes projecting from the middle of the two ends, which probably serve the same purposes as the differently shaped appendages of the ova of the shark and skate.

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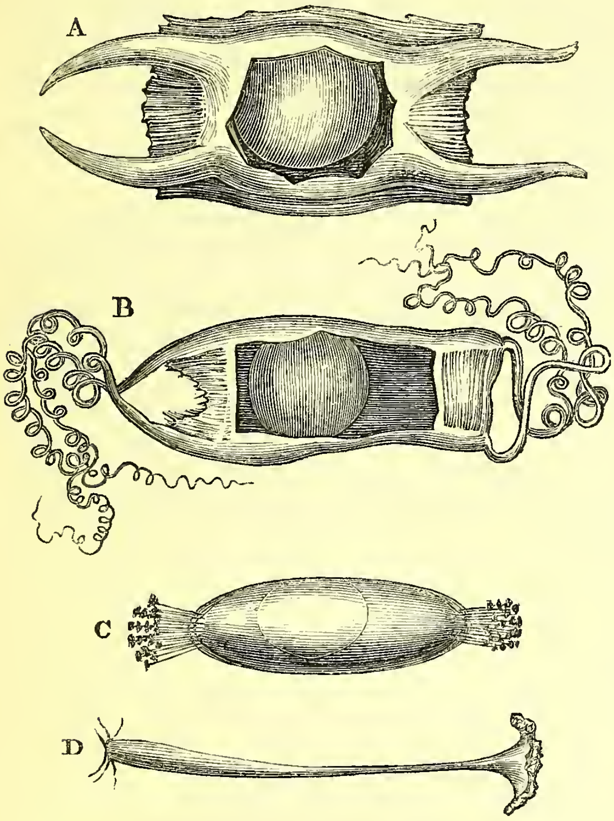
* See on this subject the works of Hewetson and others.

Fig. 33.



External form of ova of Oviparous Cartilaginous Fishes.

A. Ovum of the common skate fish, a portion removed from one side of the coriaceous envelope to show the yolk floating in the white: one-third the natural size.

B. Ovum of the shark, squalus catulus, also opened: half the natural size.

C. Ovum of the Myxine glutinosa, entire: natural size.

D. Enlarged view of one of the 25—30 tubular funnel-shaped processes from the same ovum; the attached end is at D.

In birds, it is well known that the yolk and germ, with their enclosing vitelline membrane, are produced in the ovary, while the albumen, chalazæ, membrane, and shell are more rapidly formed and are added during the passage of the egg through the oviduct. It is by an entirely similar process that these accessory parts are formed in the scaly reptiles, the eggs of which agree with those of birds in the most essential points. The albumen, however, is generally in less quantity and softer, and the twisted chalazæ have not been observed. The membrane which immediately covers the albumen has the same structure as that of the bird's egg; and the calcareous shell, when it exists, as in turtles and crocodiles, is more porous and thinner.

In cartilaginous fishes there is also a glairy albumen investing the yolk, and secreted from the oviduct. In most animals of the second group, or with the large-yolked ova, the vitelline substance consists almost entirely of oily and albuminous matter enclosed in organised cells, the nature of which differs, as previously explained, in the vicinity of the germ and in the other parts of the yolk; this substance contains, besides, the peculiar colouring matter which has given the name to this part of the egg. In all of them a cicatricula exists, which is the seat of the germinal vesicle, and of the first formation of the rudiments of the embryo.

The ovum of the frog, when newly expelled from the oviduct of the parent, consists of the yolk-ball, closely surrounded by a tough layer of peculiar albuminous matter deposited on it in the course of its passage through the oviduct. This substance has the property of imbibing a large, but yet a limited, quantity of water whenever it is immersed in it; and thus, within a short time after the expulsion of the egg from the female, the external substance has assumed a gelatinous consistence, and has enlarged to such an extent as to be on every side equal in thickness to the diameter of the dark-coloured yolk within. I shall have occasion afterwards to state more particularly the important relation which subsists between this process of imbibition and the action of the spermatic substance in fecundation. In the common frog, the ova are thus united in large masses, floating in the water of stagnant pools or rivulets: in the common toad, they are united in long cords, which become entangled among aquatic plants.

In the newts, the external covering of the ovum is membranous, homogeneous and transparent, and of an elongated oval shape, and there is merely fluid intervening between it and the spherical yolk and its membrane; but when the ova are deposited by the parent in the folded leaves of water-plants or other situations, a small quantity of a peculiar glutinous matter, not readily acted on by water, is excreted along with the ova, which serves to fix the ova in a suitable place during the development of the young.* Various examples of a similar kind occur among the oviparous animals of the invertebrata, more especially among insects and mollusca, when the ova are destined to remain exposed, and require protection during a considerable time before development takes place.

In batrachia the yolk is variously coloured in different species: thus, in the common frog, toad, and some others, the surface or germinal part of the yolk is of a black or dark-brown colour, owing to a deposit of pigment granules in the cells of the germinal layer, while the remainder of the yolk internally is grey. In some other batrachia the colour is light brown. In the larger water-newt, or triton, the yolk is of a brilliant light yellow; while in the smaller one, or lissotriton, it is ash-coloured. In the land-newt, which is ovoviviparous, the yolk is of considerable size, and of a dark yellow, approaching to orange.

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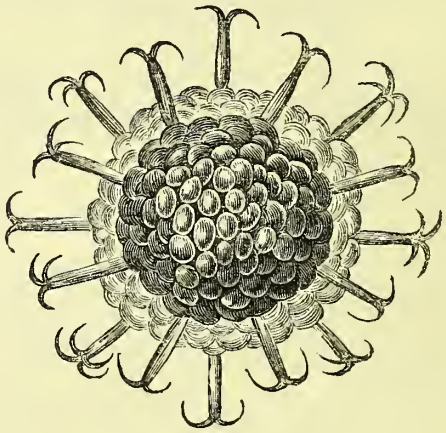
* See the interesting description of this process by Rusconi, in Amours des Salamandres Aquatiques; Milan, 4to. 1821. I have often confirmed his observations on this process in ponds, and with animals kept in vessels in the house.

In osseous fishes, which are almost all oviparous, the ovule receives, apparently in the ovarian capsule itself, before leaving that cavity, an external covering (or chorion) of considerable firmness. This membrane appears to consist of a substance deposited on the external surface of the vitelline membrane, and becomes coagulated under the action of water ; so that its density increases greatly after the ova are deposited, while it is separated at the same time from the yolk by the imbibition of water. The ova are in spawning either deposited separately, or are united in chains or bundles, and in some less common examples* in peculiar nidamental structures, more after the manner of some of the mollusca. The structure of the ovarian ovule, or yolk, and its relation to the germ, differs somewhat from that of the batrachia ; for while in the latter animals the yolk substance consists of granules and cells of nearly uniform size, and the germinal layer covers the greater part of the surface, in osseous fishes this layer is more circumscribed, not extending at first over more than a third, or, at most, a half of the yolk, and the remainder of the yolk, which contains a much greater quantity of transparent fluid than in most other vertebrate animals, presents almost invariably a peculiar heap or mass of large oil globules, which float to the upper part of the fluid below the germinal layer.†

The minute ovula of mammalia, when they have reached maturity in the Graafian capsules of the ovary, are nearly spherical bodies, of from $\frac{1}{120}$ to $\frac{1}{300}$ of an inch in diameter, and consist of a mass of finely granular yolk substance, more loose in the interior and more dense towards the surface, and enclosed in a thick firm and transparent vesicular envelope, the vitelline membrane, or so-called zona pellucida. While still within the Graafian capsules, they occupy a situation near the most projecting part of the capsule, or towards the external surface of the ovary, being there imbedded in a layer of granular cells, the *discus proligerus* of Von Baer, which lines the ovicapsule, and lies on the exterior of the clear coagulable fluid with which this capsule is filled. A portion of this lining membrane of granular cells, remains adherent to the ovum after it leaves theGraafian capsule, and has passed into the Fallopian tube ; but as it descends towards the uterus, these cells gradually loosen and fall away from the surface of the ovum, the zona pellucida or vitelline membrane of which is thus finally left free. In the farther progress of its descent, there is formed, in some mammalia at least (rabbit), on the surface of the zona by a new deposit, in others, perhaps, by conversion of the zona itself, the external membrane of the ovum, which at a later stage constitutes the chorion. But, in accordance with the destination of the ovum in this tribe of animals for true uterogestation, this external membrane has then no longer the character of mere inactive limitation of the exterior of the ovum, or defence from injury, which belongs to it in the lower animals ; but it becomes an organised and growing texture of active functions, which is the more immediate means of uniting organically the blood-vessels of the mother and fœtus, in such a manner as to allow of the transmission of nourishment from the one to the other.

Varieties of form of the ova among the invertebrata are too numerous to allow of their being described in this place. In the greater number, an external envelope, besides the vitelline membrane, exists ; but it must be admitted, that there are some in which these two coverings cannot be distinguished. In some, as in insects, arachnida, polypes, &c., the chorion, or outer surface, presents peculiar markings, ridges, tubercles, or long spines, and is strong and opaque ; in others, it is smooth, delicate, and transparent, so as to allow the whole internal structure of the ovum to be seen through it, and thus to afford most favourable opportunities of witnessing the early changes of development. In most of the invertebrata the germinal part of the yolk covers the whole, or a considerable part, of its surface ; they present, however, great varieties of colour and structure, and may, probably, belong to various modifications of the second and third groups before distinguished.

Fig. 34.



Ovum of Cristatella mucedo.

(From Turpin, Annal. des Scien. Nat. 1837, tom. vii.) Showing peculiar spinous projections from the outer shell.

It does not appear that any essential difference has yet been observed in the structure of the ova of those animals which are subject to alternate generation, and those of animals in which the adult form is directly developed from the ovum.

§ 3. Of the ovary in general as the formative organ for the ova of animals.

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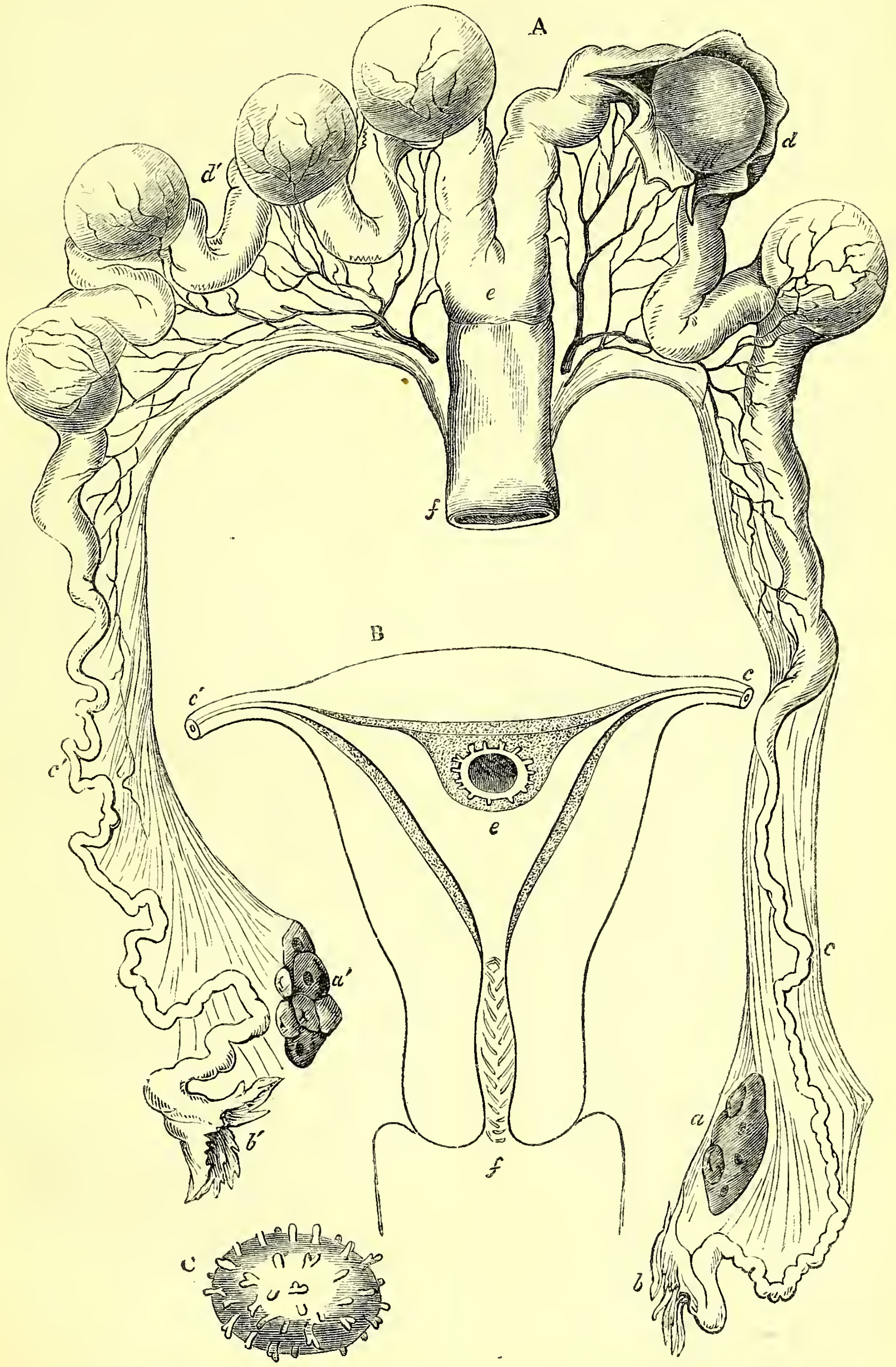
* As Gobius. See Prof. Owen's Lectures on the Compar. Anat. and Physiol. of Vertebrated Animals, part i. p. 304. A. Hancock on the Nidification of the Gasterosteus aculeatus, &c., in Annals of Natural History, Oct. 1852.

† See a paper by Dr. Davy on the chemical properties of the vitellus of Osseous fishes in Trans. Roy. Soc. for 1851.

The name of ovary is in all animals applied to the organ, however varied in its structure and relations, in which the ova are formed. As already indicated, however, it is to be observed, that in the higher animals, it is only the ovule, or yolk, with its germinal vesicle and enclosing membrane that is formed in the ovary, while the external or cortical parts of the ovum are added to these in their descent through the female passages after leaving the ovary. There are some examples in which it would appear that the whole

Fig. 35.



Relation of the ovaries, ovum, oviduct and uterus in Mammalia.

A. Gravid uterus, &c. of the rabbit, ten days advanced in pregnancy; *a′ a*, right and left ovaries, four corpora lutea in the right, two in the left; *b′ b*, fimbriated openings of *c′ c*, the Fallopian tubes; *d′ d*, the right and left cornua of the uterus; *d′*, with four dilatations from contained ova, *d*, with two dilatations, one of which is opened to show the ovum; *e*, the body of the uterus; *f*, the vagina.

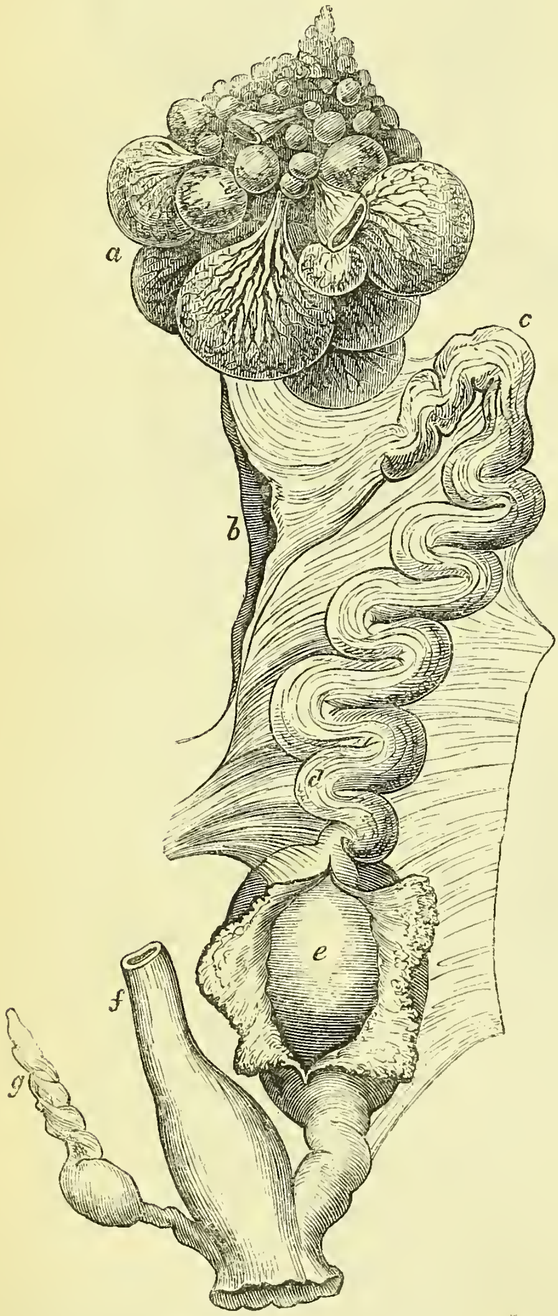
B. A diagrammatic transverse section of the human uterus, at twelve or fourteen days after conception, somewhat less than the natural size; *e*, the uterine cavity, near which the ovum with its villous chorion is involved in the substance of the decidua indicated by the dotted shading; *c′ c*, the Fallopian tubes cut short, by one of which the ovum had previously descended while still of small size.

C. Enlarged view of the exterior of the human ovum, of twelve or fourteen days after conception, showing the villi of the chorion projecting from its surface.

formative process of the ovum, including the addition of the external coverings, is completed within the ovary; and, on the other hand, there are a few instances in which, as in the trematoda and cestoid entozoa, the germinal vesicle and yolk substance of the ovule are formed in separate organs, instead of in the usual manner entirely in the ovary.

The varieties of the ovaries in different animals may be considered under two heads —viz., 1st. Their relation to the passages or outlets as influencing the mode of discharge of the ova from them; and 2nd, their internal structure as related to the form of the ovum produced.

Fig. 36

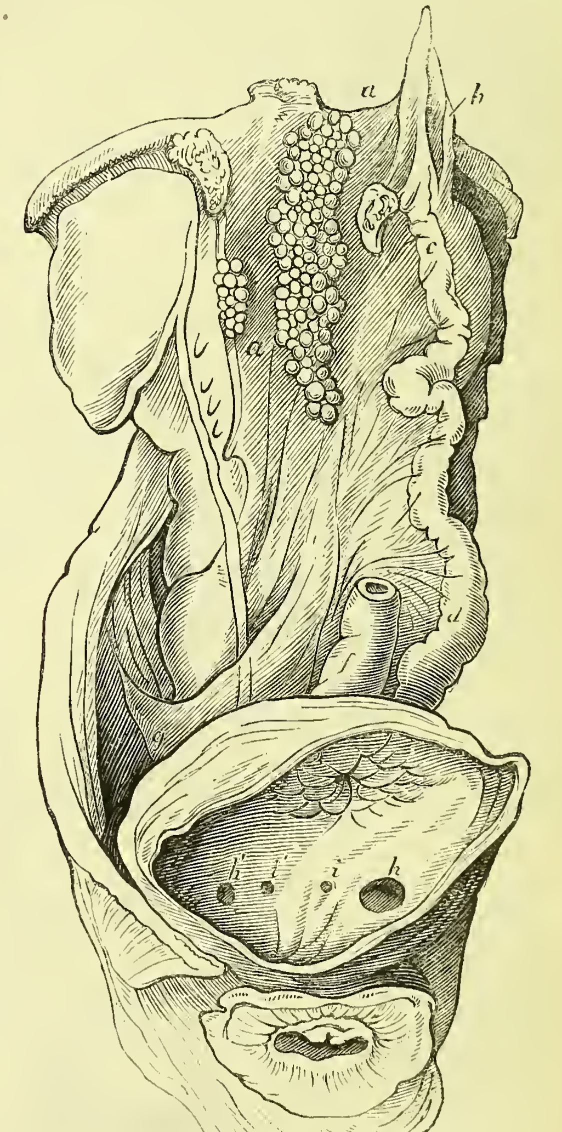


Ovary and oviduct of a laying Fowl, killed twelve hours after laying the last egg.

a. Left ovary; *b*, opening of the infundibulum of the oviduct; *c*, *d*, glandular portion of the oviduct; at *d*, the isthmus; *e*, an egg in the uterine portion of the oviduct, in which the shell is begun to be deposited; *f*, the rectum, ending in the cloaca; *g*, the undeveloped right oviduct occasionally met with.

a. Relations of the form of the ovaries to the discharge of ova.—In the majority of vertebrated animals the ovary or ovaries are quite detached from the conducting tube or oviduct; the ovules are formed in close capsules of the ovary, by the bursting or fissure of the wall of which they escape; the oviduct opens at its upper end into the abdominal cavity, and there receives the ovum which has been discharged from the ovary. This is the general arrangement in mammalia, birds, reptiles, amphibia, and cartilaginous fishes. There is some difference in the form of the ovary in the higher and lower of these animals. In mammalia and birds, in chelonia and the crocodiles among the reptiles, and in cartilaginous fishes the ovary is more or less solid, and the ovules are developed in capsules which project towards the external surface; but in the lizards

Fig 37.

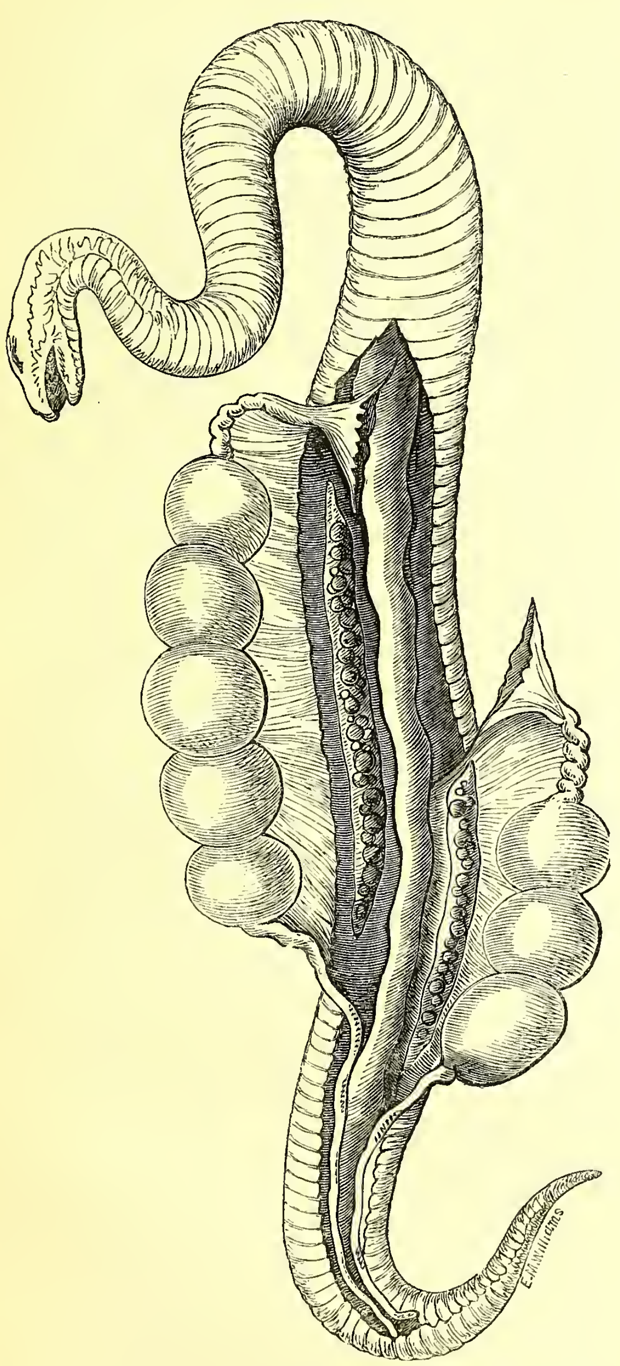


(*From Carus and Otto.*)

Female of the Falco buteo opened, showing the left larger oviduct and ovary, and the smaller right oviduct and ovary. *a' a*, the right and left ovaries; *b*, the left infundibulum; *c*, *d*, the left oviduct; *f*, the rectum, ending in the cloaca, which has been opened, showing at *h' h* the openings of the right and left oviducts, and at *i' i* those of the ureters; *g*, the vestige of the right oviduct.

and serpents, and in the batrachia, this organ is hollow, and the capsules in which the ovules are formed burst in dehiscence into an internal cavity, whence the ovules escape into the abdomen by the rupture or opening of the sack of the oviduct, generally at one, but sometimes, as in the frog, at a greater number of places. In the higher animals, in which the ovules escape from the external surface of the ovary, their entrance into the oviduct is in general secured by the temporary apposition of the dilated upper end or infundibulum of the oviduct to the ovary, or the capsule containing a ripe ovule; in the other animals, in which the ova come from the interior of the hollow ovary, the apposition of the oviduct does not appear to be so direct, and there are various other means by which the ova, when they have escaped into the abdominal cavity, reach the open extremity of the oviduct.

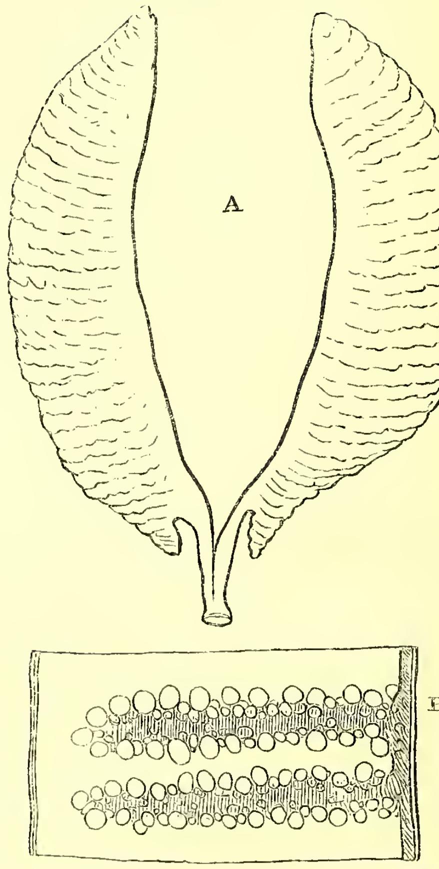
Fig. 38.



Common adder, in which the ova have descended to occupy both oviducts, five in the right, and three in the left: the infundibulum is shown in each oviduct; *a' a*, the right and left ovaries, each forming a sac, opening anteriorly near the infundibulum for the discharge of the ova, which, when ripe, fall into the interior of the sac, and thence pass into the oviduct.

It is in the class of fishes that the transition occurs from the higher to the lower type of organisation of the ovaries and oviducts. In all of them the ovules are formed in ovarian follicles, and escape by dehiscence from these follicles; but there are several modifications of the relation between the oviduct and ovary among them. 1st. In the sharks and rays, as already stated, the arrangement is nearly similar to that existing in higher animals. The ova, which are of large size, come to maturity singly, or in small numbers at once: on being discharged externally from the ovarian capsules, they pass into the oviduct, and there receive a considerable addition from this organ. The majority of them, as previously stated, are oviparous, and in them a hard covering is formed by a peculiar glandular organ connected with the oviduct; in a few which are ovoviviparous, as the common dog-fish, torpedo, &c., the external covering of the ovum is membranous and soft. 2nd. In the sturgeon and in the lamprey the oviduct is very short; still, as it opens superiorly into the abdominal cavity, the relation may be considered the same as in the previous examples. 3rd. In the genus salmo and in

Fig. 39.



Ovaries and oviduct of an osseous Fish.

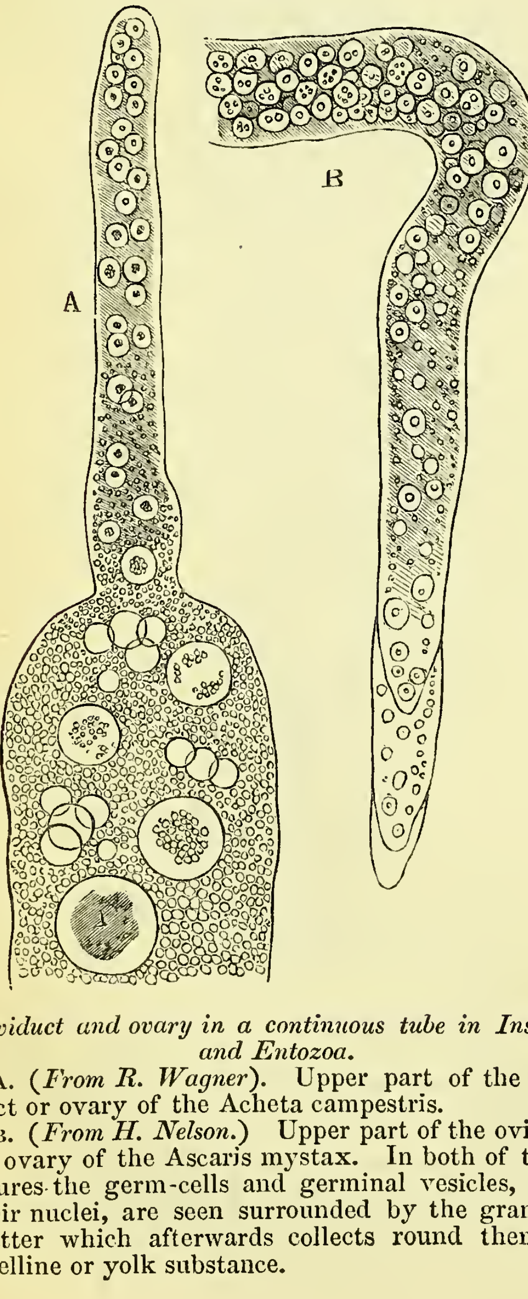
A. Sketch of the two largely developed sacculated ovaries of an osseous fish, with the short oviducts proceeding from near their posterior extremities.

B. Diagrammatic section of a portion of the ovarian sac, showing two of the ovarian plates, from which the developed ova hang in small pediculated vesicles or ovisacs.

the eel among the osseous fishes, the oviduct is entirely wanting, and the numerous ova, which are discharged by external dehiscence from the ovary into the cavity of the abdomen, escape from that cavity by an orifice (porus abdominalis) situated on each side close to the anus. 4th. In other osseous fishes, the ovary and oviduct are united, or the ovary forms a saccular organ, in the interior of the wall of which the ovicapsules are situated, occupying a variable extent of it in different genera ; and the wall of the oviduct, usually very short, is continued from that of the ovary to the outlet from the animal's body. The ova, therefore, which drop by internal dehiscence into the cavity of the ovary, pass directly out by the short oviduct in the laying of the spawn. Most osseous fishes are oviparous; but in a few, as the viviparous blenny, the anableps, paecilia, and some siluroids, the ova, on escaping from their capsules into the cavity of the ovary, remain there during the development of the embryo.

In the invertebrate animals there are very many varieties in the form and relations of the productive and conducting parts of the female generative organs. Three principal varieties may be distinguished among them 1st. A form similar to that just now described as generally prevalent among osseous fishes, in which the ovary and oviduct are continuous, but in which the ova, being formed in ovarian capsules, are dropped by dehiscence into the upper part of the oviducts. Such is still the structure in cephalopoda and some other mollusca. 2nd. A form in which the oviduct may be said to be, as in the last, continuous with the ovary, but in which there is no true dehiscence of the ovules from ovarian capsules, as they are formed at once in the internal cavities of the ovary, which directly open into, or are mere prolongations of, the oviducal tubes. In this form the oviducts may be considered to stand in the relation of excretory ducts to the ovarian glands. In many of this class the ovaries present very various forms ; in some the continuity of the ovarian and oviducal tubes is very obvious and simple, as in the nematoid entozoa, insects, &c. ; while in others, the ovary is more complex and racemose, and the oviducal tubes comparatively simple. 3rd. That form in which the ovaries are variously disseminated over the body of the animals, and in which there are no true oviducts, but the ova escape on various parts of the internal or external surface of the body.*

Fig. 40.



Oviduct and ovary in a continuous tube in Insects and Entozoa.

A. (*From R. Wagner*). Upper part of the oviduct or ovary of the Acheta campestris.

B. (*From H. Nelson.*) Upper part of the oviduct or ovary of the Ascaris mystax. In both of these figures the germ-cells and germinal vesicles, with their nuclei, are seen surrounded by the granular matter which afterwards collects round them as vitelline or yolk substance.

b. Structure of the ovaries themselves, as related to the production of the ovula. — In mammalia these organs consist of a pair of solid oval flattened bodies, attached by intervening fibrous tissue to the posterior surface of the broad ligaments of the uterus, and are covered completely, excepting at this attached part, by peritoneum. Below this serous covering there is also a layer of firm fibrous tissue, or *tunica albuginea.* The internal substance, or parenchyma, or stroma, as it has been called, consists of a firm basis of fibrocellular texture, of considerable vascularity. The fibres, as well as the blood-vessels of this substance, radiate principally from the attached border of the organ towards the opposite, or free side, and the rest of the surface. The ovicapsules, or so-called vesicles or follicles of De Graaf, in the human ovary, are situated in this stroma; and at or after the period of puberty are found of some size; a variable number, from twelve to thirty, or more, being of from $\frac{1}{20}$ to $\frac{1}{6}$ of an inch, and a few even a little larger. These membranous vesicles, filled with fluid, are situated chiefly towards the surface of the free side of the ovary. A larger number of undeveloped capsules, of minute size, also exist in the

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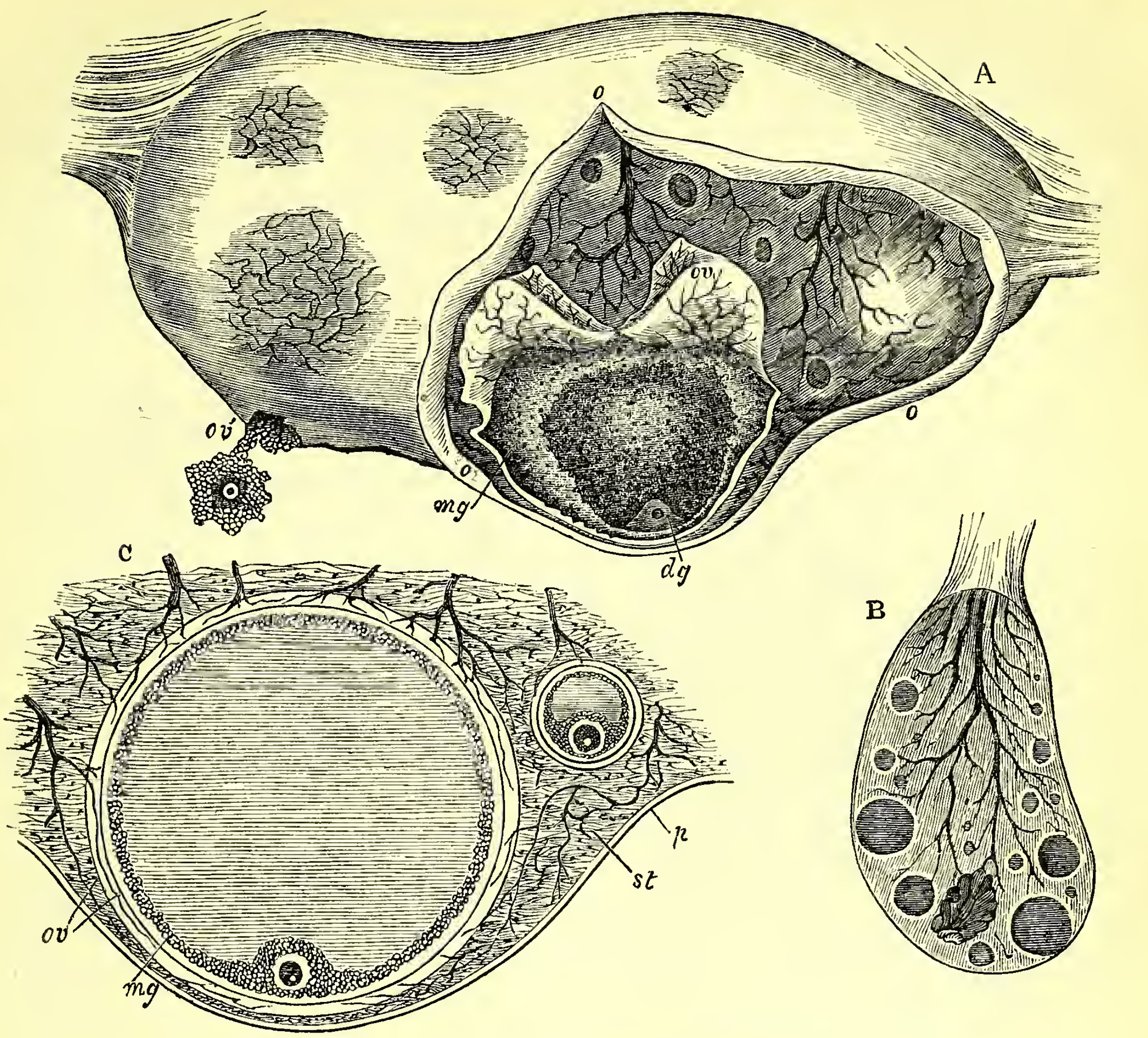
* See Von Baer's Entwickelungsgesch. der Thiere ; Owen's Lectures on Invertebrate Animals, 1843, and on Fishes, 1846 ; Rathke (on Development of Fishes, &c.), in Geschichte der Thierwelt, Th. 3.; J. Müller (on Sharks), in Mem. of Berlin Acad. 1842; John Davy (on the Torpedo), in Philos. Trans. for 1834; and the works of Von Siebold and Stannius, R. Wagner, Carus, and others on Compar. Anat. See also in this Cyclopædia, the articles Monotremata, Pisces, Reptilia, and Organs of Generation.

Fig. 41.



Relation of the ova and ovaries in Mammalia.

A. (*From Coste, as reduced by Longet.*) Human ovary, enlarged four diameters, partially dissected at *o o o*, to show the Graafian follicles in the ovarian stroma: one of these, more advanced, has had its double tunic, *o v*, cut into and reflected; the granular membrane, *m g*, has also been partially opened, showing the thickened portion or granular disc, *dg*, in which the ovum is imbedded near the most projecting part. At *o v'*, another Graafian follicle has been burst, and the ovum in its granular disc is seen expelled from it.

B. Transverse section of human ovary, to show the general arrangement of the developed Graafian follicles towards the surface; twice the natural size.

C. Diagrammatic representation, in section, of two Graafian follicles, in different stages of advancement in the ovary of a mammifer, enlarged about ten diameters. *p.* Peritoneal covering of the ovary, *s t*, ovarian stroma; *o v*, the two layers of the ovisac; *m g*, membrana granulosa, near which is the discus granulosus, with the ovum imbedded.

stroma; and it has been observed, that these are present from a very early period in the ovaries, as first noticed by Carus, and since by myself and others in the child at birth.

The more developed of these ovi-capsules are enclosed by a strong theca or membrane, consisting of two layers; the external thinner and firmer, of a fibrous and vascular structure, the internal thicker and softer, of a fibro-cellular structure and also of considerable vascularity. The capsules are filled with a fluid nearly transparent, which coagulates under the action of heat; and inside the theca, or lining it and covering the fluid, there is a layer of nucleated cells united together in the form of a soft, easily-lacerated membrane, somewhat like an epithelial lining of the capsule. It is in this cellular layer (*tunica granulosa* of Von Baer) that the ovum is placed, being situated in the thicker portion of it (*cumulus proligerus*), directed towards the surface of the ovary.

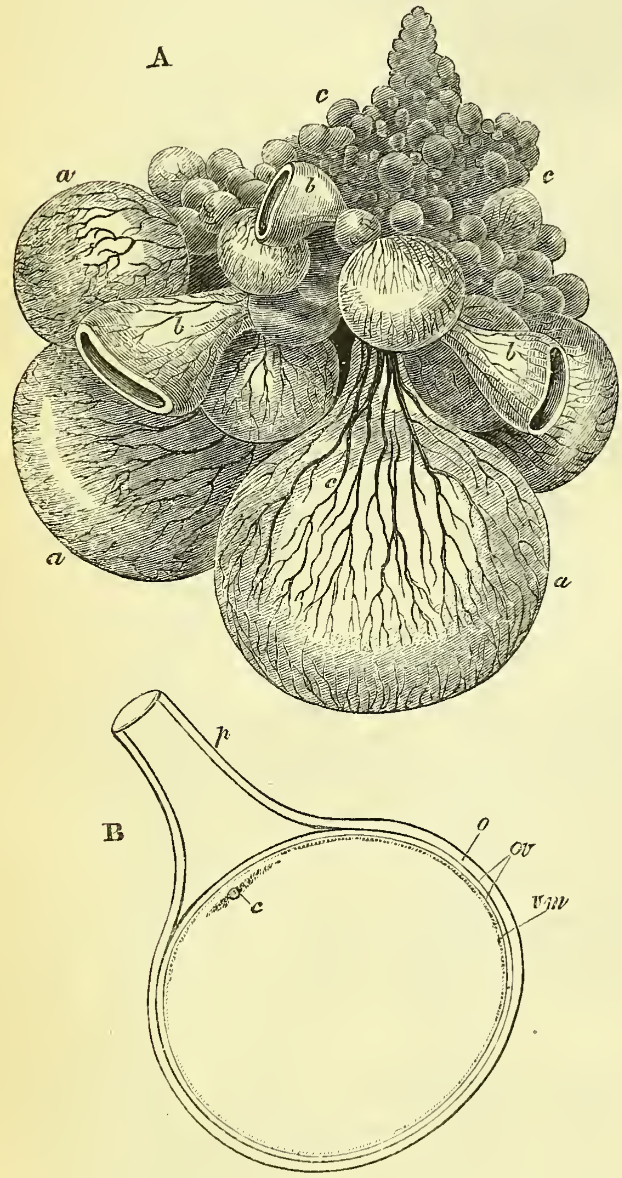
When one of the ovicapsules and its contained ovule has reached maturity, which takes place in one or more of them at regularly recurrent periods, besides the swelling of the ovicapsule itself from the increase of its fluid and other causes, the stroma of the ovary between the capsule and the surface undergoes considerable thinning, and the ovicapsule comes thus to project more immediately from the surface of the ovary. An increased vascularity is also apparent in the same situation; and finally a small circumscribed fissure near the middle of the most projecting part occurs, allowing the escape of the ovule and the granular layer and fluid from the ovicapsule.

The ovule, surrounded by a portion of the cellular layer in which it was embedded, is received by the open fimbriated extremity of the Fallopian tube.

The empty ovicapsule now undergoes a remarkable change by the deposit in its interior of the substance termed corpus luteum, the quantity and nature of which vary greatly according as the escape of the ovule is followed or not by pregnancy. Of this change more will be said hereafter. The result in both cases is the ultimate closure and obliteration of the ovicapsules.

In birds, scaly reptiles, and cartilaginous fishes, the greater size of the ovules when in a state of maturity is connected with a modification of the structure of the ovary and the ovicapsules.

Fig. 42.



Relation of the ova to the ovary in Birds.

A. Ovary of a fowl, showing at *a a a* the most developed ova hanging from the ovary in their pediculated capsules; the non-vascular bands are seen on their most projecting sides; at *b b*, the empty capsules or calyces of ova that have been previously discharged; at *c c*, the more compact part near the root of the ovary, where the ova are less developed.

B. Diagrammatic section of one of the most advanced of the capsules; *o*, the extended ovarian substance forming the capsule; *p*, its pedicle; *c*, indicates in this and the preceding figure the most common position of the cicatricula or germ-disc and vesicle; *o v*, the two layers of the ovicapsule or ovisac, into which the blood-vessels penetrate: the dotted line *v m*, marks the vitelline membrane.

Previous to the age for breeding, the ovary of birds — in which animals only one ovary and oviduct is usually developed or attains to functional activity — is a solid organ of a less firm texture than that of mammalia, and is adherent to the vertebral column in the middle of the dorsal region. It contains at an earlier period a much greater number of ovicapsules of a considerable size than are perceptible in mammalia. The stroma or ovarian substance is in less proportion, therefore, to the ovicapsules and ova.

As the ovules become more developed, they increase rapidly in size; and we then perceive that they bear a different relation to the ovicapsules from that which has previously been described in mammalia, as they fill completely the ovicapsules, and there is no fluid or loose cellular layer between the outer surface of the vitelline membrane and the lining membrane of the theca.[*] As some of the yolks approach maturity their increase in size is proportionally much greater, and the theca or ovicapsule, and along with it the ovarian substance, is distended in like proportion; and in this manner the ovary of the fowl at the breeding season has lost its appearance of compactness or solidity, and seems to be composed almost entirely of a larger number of pediculated ovarian capsules of the most various sizes, filled with the yolks or ovules in all stages of development. Nevertheless, a little attention shows the solid part of the ovary still remaining at the part attached to the vertebral column, forming the ground, as it were, from which the pedicles of the enlarged capsules spring, and containing still a very large number of minute undeveloped ovules in their correspondingly small ovicapsules.

The large ovicapsules of the developed ovary of the bird consist of two layers, which are loosely united together by blood-vessels and binding tissue towards the pedicle and over the greater part of the capsule, but are more firmly knit together at the free border. At the latter place the blood-vessels of the theca, which are on all the other parts distributed in wide or comparatively large channels very thickly set, suddenly become so small and delicate as to give, at first sight, the appearance of an absence of vascularity in the course of a band of about $\frac{1}{6}$th of an inch in breadth, and extending across a large portion of the free circumference of the capsule.[†] This is the so-called stigma, at which, when the ovule is to escape from the ovary and to be transferred into the oviduct, the rupture of the theca occurs.

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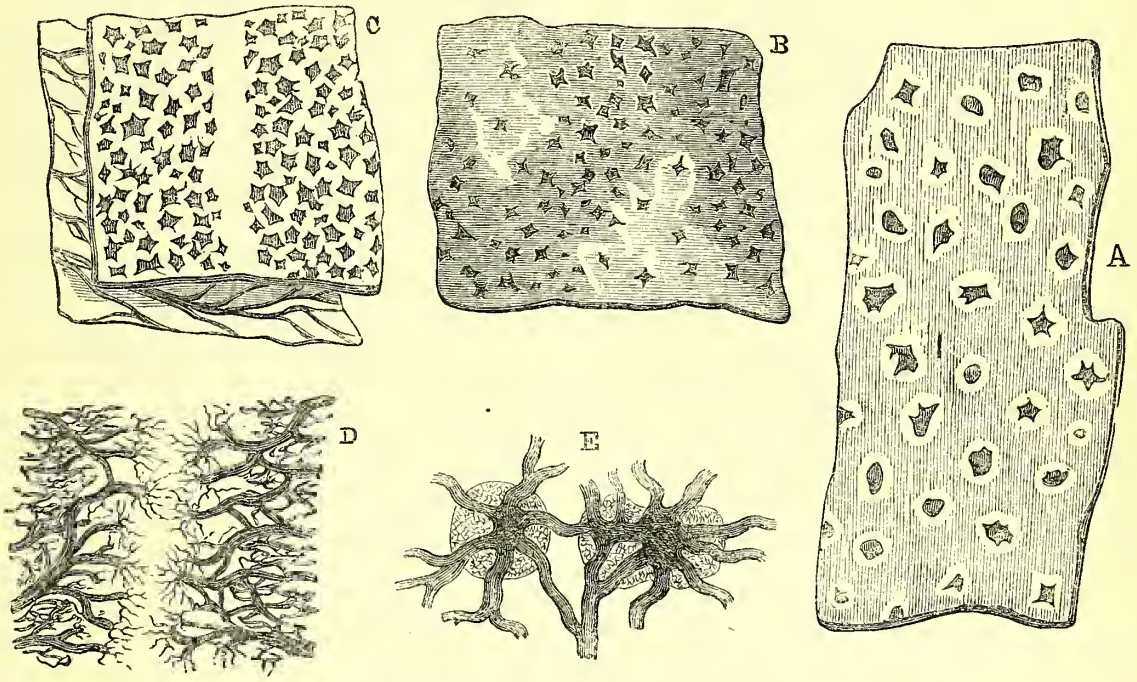
[*] There may probably be an epithelial lining of this membrane. See H. Meckel's paper, afterwards referred to, Zeitsch. für Wissensch. Zool. vol. iii., 1852, p. 420.

[†] The length of this band or stigma is about equal to the long diameter, or a third of the circumference of the capsule at its widest part. It is sometimes crossed by a second band of the same kind.

Each developed ovule, therefore, in these oviparous animals, comes to be contained in a pediculated capsule, which is formed by the extension of the substance of the ovary; but from the great extent to which the dilatation of the capsule occurs, the true ovarian stroma is reduced to a very small amount, and scarcely more remaining than the theca of the capsule itself and the ovarian coverings.

In the other animals possessing the large yolked ova, nearly the same structure of the ovary prevails. In chelonia and crocodiles, it is indeed almost identical with that in birds. In lizards and serpents, the hollow state of the ovary produces some difference in the general form; and in cartilaginous fishes (sharks and rays) other differences in the structure of the ovary may exist; but in all these animals the essential points of relation between the ovarian substance and capsules, and the large ovules, are the same as that now described in birds.

Fig. 43.



Structure of the ovisac in the Fowl's ovary.

A. Inner surface of a portion of the ovisac of a fully-developed ovarian capsule, magnified about six diameters, showing an appearance which might be mistaken for glandular depressions produced by the peculiar disposition of the veins.

B. The same, from a calyx from which the ovum has been discharged some days before; a whitish flaky membrane is deposited on portions of the surface.

C. The same, from an undeveloped capsule of a quarter of an inch in diameter, across the stigmatic band.

D. The disposition of the blood-vessels near the stigmatic band, which seems at first sight non-vascular, but is in reality traversed by ramifying small vessels proceeding from the neighbouring larger veins, and crossing the stigmatic band.

E. Two of the large mouths of the veins, which give the semblance of follicular pits represented in A and C, but which are quite closed, with the smaller vessels ending in them, as seen from the inner surface of the ovisac.

The lining membrane of the ovicapsule of birds is thick and tough, and on its inner surface presents a soft appearance somewhat similar to that of a mucous membrane. In examining the inner surface of this membrane, Dr. Sharpey and the author had their attention arrested by an appearance such as might, on first sight, be attributed to a number of follicular or glandular pits. This appearance, as we first observed it, is represented in *fig.* 43. (A, B, C) as it was seen in a fully-developed capsule—in one a third of an inch in diameter—and in a calyx from which the yolk had been discharged some days previously. We supposed, indeed, at first that the appearance depended on the presence of the orifices of follicular depressions or glands on the inner surface of the membrane. A more attentive examination of this membrane by Dr. Sharpey has shown that the appearance is not due to depressions of the inner surface of the membrane or to the mouths of follicles opening upon it, but is caused by a peculiar form of the blood-vessels seen through the entire and smooth inner surface of the membrane. The apparent depressions are in fact the sudden terminations or beginnings of veins of considerable size seen through a delicate and transparent portion of the membrane which closes them towards the inner surface. They may be made very obvious by merely coarsely brushing the smooth blunt edge of any instrument over the membrane, and thus causing the blood to flow from the vessels in other parts in these sinuses or dilated veins.

It would appear that the smaller capillary vessels in which the arteries terminate, in approaching the inner surface of the capsule, ramify with considerable minuteness, and at each of the marks or apparent depressions referred to suddenly fall into or end in the comparatively large veins which constitute the hollow spaces. The ends of these veins, then, look towards the inner surface of the membrane; and the appearance of a divided cavity in some of the supposed follicles is merely caused by two or more veins meeting in a common dilatation at this place. The capillary vessels, in passing into these large commencements of the veins seem to converge from its circumference to its centre.

In the enlarged ovarian capsules of the turtle, a somewhat similar arrangement may be observed; but I have not had an opportunity of tracing its relation to the blood-vessels; nor have I had the means of ascertaining whether anything of the same kind exists in other reptiles with large yolks. In the skate I have not been able to perceive any similar arrangement; and in the Graafian vesicle of mammalia the lining membrane presents internally a smooth surface destitute of any appearance of depressions or of peculiar venous sinuses.

The appearance which I have just now described had not escaped the notice of Von Baer; for at p. 23 of his work on development, he mentions the existence of clearer points in the inner membrane of the theca, and states his opinion that they may be open mouths of blood-vessels, by means of which the yolk may be nourished by the direct access of blood to it.

In the naked amphibia and osseous fishes, the ovaries (of which the general form has been previously noticed) present a still greater decrease in the proportion of the stroma to the ovicapsules and ova. These capsules are themselves also of much more delicate structure than in the higher animals; but the relation of the ovules to the ovicapsules in their formation, and the mode of their escape by the rupture of the theca, are essentially analogous to those of birds and reptiles. In the earliest condition, it is true, the ovary may present a greater amount of solidity in some of these animals; but from the prodigious number of the germs of the ovules and the small quantity of the ovarian stroma, as soon as the ovary has made some progress in development, it acquires the appearance rather of a mere mass of ova connected together by a membrane and fine thread-like pedicles, than of a solid or consistent organ containing them. The delicate ovicapsules containing the ovules embrace them closely as in the large-yolked group of animals, there being little or no fluid between the capsules and the vitelline membrane.

The structure of the ovaries in the invertebrate animals presents so many varieties that it would occupy too much space to allude to them here. I refer the reader for information regarding them to the article Organs of Generation, and others on particular classes and orders of animals in different parts of this work. For our present purpose the structure of these organs has been sufficiently indicated in the previous section.

In conclusion, it may be right to recapitulate the general nature of the ovary or formative organ in its relation to the production of ova. A comparison of the forms previously indicated leads to the general view that the ovary is to be regarded as analogous to the glandular organs. In the great majority of animals highest in the scale, the ovisacs are close follicles from which the product of formation (or secretion) escapes by the bursting of the wall of the follicle — in the highest animals, on the external surface of the organ, in those coming next in the series, towards an internal cavity. In other instances, principally among the lower animals, the structure is more analogous to that we are accustomed to consider as characteristic of the true glands, in which the secreted cellular product is formed within the same or a continuation of the tubular ducts themselves by which they make their escape. The more complex structure of the capsules in which the large-yolked ovules are produced in birds constitutes a special apparatus, which, though without follicular complication, may be looked upon as a modification or higher degree of development of the glandular structure of the ovary, provided for the rapid formation of the larger mass of nutritive substance which is present in these ova.

§ 4. *More detailed description of the ovum of birds as the type of the 1st group.*

Having in the previous section given a sketch of the general resemblances and differences observed among the ova of various animals, I now proceed to describe more in detail an example from each of the three groups previously distinguished, and more particularly those of Birds and Mammalia, which demand the greatest share of our attention in the study of development; and first as to the ovum of the common fowl.

Quantity of matter, composition, &c. — The average dimensions of the fowl's egg in this country are the following: The long diameter 2¼ inches, short diameter 1¾ inch. The average weight of eggs of this size is a little more than 2 oz. avoird., or 920 grains.*

The extremes in weight which I have observed among eggs of the fowl naturally formed are 750 and 1060 grains. Double-yolked eggs are, as might be expected, much larger, reaching often a weight of 1400 grains, or 3¼ oz.

The yolk weighs about a third of the whole; the albumen, membrane, and shell forming the remaining two thirds. These parts of the egg are in the following proportions to each other in 100 parts; the albu-

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* The following is a comparative view of the average size and weight of the eggs of the common fowl, duck, turkey, and goose.

	Length	Breadth	Weight	
	(in inches).		(in grains).	
Fowl -	2·25	1·7	920	nearly 2 oz.
Duck -	2·5	1·75	1100	2½ oz.
Turkey	2·7	1·9	1300	3 oz.
Goose -	3·3	2·4	2600	6 oz.

men 58, the yolk 31½, and the shell with its lining membrane, 10½.

When eggs are kept exposed, they gradually sustain a small loss, due chiefly to the evaporation of water, and amounting to about one grain per day. When putrefaction ensues, an additional loss from chemical changes occurs.

During incubation, the loss of weight is more considerable, amounting in twenty-one days to 16 or 17 per cent., or nearly one sixth of their entire substance.* The loss by an egg during incubation, therefore, is eight times as great as that which occurs in an egg kept at the usual atmospheric temperature for the same period — a circumstance which depends partly on the higher temperature, but principally on the evolution of carbon from the oily matters of the incubated egg, in combination with the oxygen of the air, or as carbonic acid, &c.

Of the 17 parts per cent. lost during incubation, not more than 5½ or 6 consist of water, and the remaining two thirds, that is 10 or 11 parts, are derived from the oily and other substances of the egg which undergo chemical changes attendant upon the process of organisation and respiration of the embryo.

By evaporation to dryness of the whole egg without the shell and membrane, about 27 per cent. of the substance are left; the oily ingredients of this residue, amounting to about 10¾, are almost all contained in the yolk, and the remaining 16¼ parts of solid matter are nearly equally divided between the yolk and the white. The yolk, therefore, is much richer in the fixed and solid parts than the white; but its specific gravity, as will afterwards be seen, is considerably reduced by the larger quantity of oily matter it contains: the per-centage of solid matter (independently of the oleaginous substance) contained in the yolk and albumen, is in the proportion of 32 in the first to 14 in the second.†

The solid residue obtained by evaporation of the white at a low temperature, amounting to nearly one seventh of the whole, consists chiefly of albumen; along with which there is also some animal matter which has hitherto been named by chemists as extractive, and a small amount of salts, which are principally alkaline sulphates, muriates and phosphates, with phosphate of lime, some free soda and sulphur.

The yolk contains little more than half its weight of water, or 54 per cent. The remaining 46 parts consist of about 17 of albumen, or analogous principles, 28 of oily matter, and 1¼ of salts. These last are chiefly alkaline muriates and sulphates, phosphate of lime and magnesia, and traces of iron, sulphur, and phosphorus. The albumen has an alkaline, the yolk a neutral, reaction.*

The membrane lining the shell consists apparently of a protein compound, analogous somewhat to that of the elastic yellow tissue.

The shell consists of earthy salts deposited in a delicate matrix of animal matter, which last constitutes not more than 3 per cent. of the whole. The earthy ingredients are in great part carbonate of lime, together with a little carbonate of magnesia, and phosphate of lime and magnesia.

Of the ingredients of the egg before mentioned, the albumen and other animal principles, together with the sulphur and salts, are no doubt more immediately employed in the growth of the embryo; while the oily matter, besides contributing, as it appears, in some part, to the same purpose, serves more directly and in greater quantity for the respiratory process, in which it is consumed largely during incubation.

The alkalinity of the white of egg appears to depend on the presence of caustic soda, which albumen has the property of separating from its carbonate.

The following tabular view exhibits in a general way the change in the relative proportion of the ingredients of the egg resulting from incubation†:—

		Fresh egg.	Incubated egg.
Shell and membrane		10·67	10·
Albumen, &c.		17·8	19·4
Oily matter, &c.		18·83	6·5
Water		52·7	47·1
Loss	Water - 5·6 Oily matt., &c. 11·4		17·
		100·00	100·00

When an egg is examined immediately on being laid and while yet warm, or still better when taken from the egg-bag of the fowl previous to laying, the yolk and white fill completely the interior; but immediately on cooling, a small space or vacuity appears generally towards the obtuse end of the egg, and this air-space increases gradually in size as the eggs are longer kept and the natural evaporation of water proceeds. This space is formed by the separation of the two principal layers of the lining membrane of the shell. During incubation the air-space increases much more rapidly; and indeed towards the end of this

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* See Prout, On the fixed Principles of the Egg, Philos. Trans. and Annals of Philos. for 1822. Also, by the same author, On the Changes of the Egg in Incubation, in the same Journal, for 1823.; and, Paris, On the Physiology of the Egg, in Linnean Soc. Trans. vol. x. p. 304, and Annals of Philos. 1821.

† See Prevost and Morin, in Journ. de Pharmacie for 1846, and Sacc, in the Eggs of the Bantam Fowl, in Annal. des Scien. Nat. for 1847, p. 69.

* Composition of the yolk, according to Gobley, in Journal de Pharmacie, 8e. sér. tom. ix. p. 174.

Water, about	53·
Vitelline, albumen, and protein compounds	16·5
Oily matters	29·
Salts, &c.	1·5
	100·0

These salts are the following — viz., chloride of sodium and potassium, sulphate of potassa, muriate of ammonia, phosphates of lime and magnesia, lactic acid, colouring matter, iron.

† From Sacc, loc. citat.

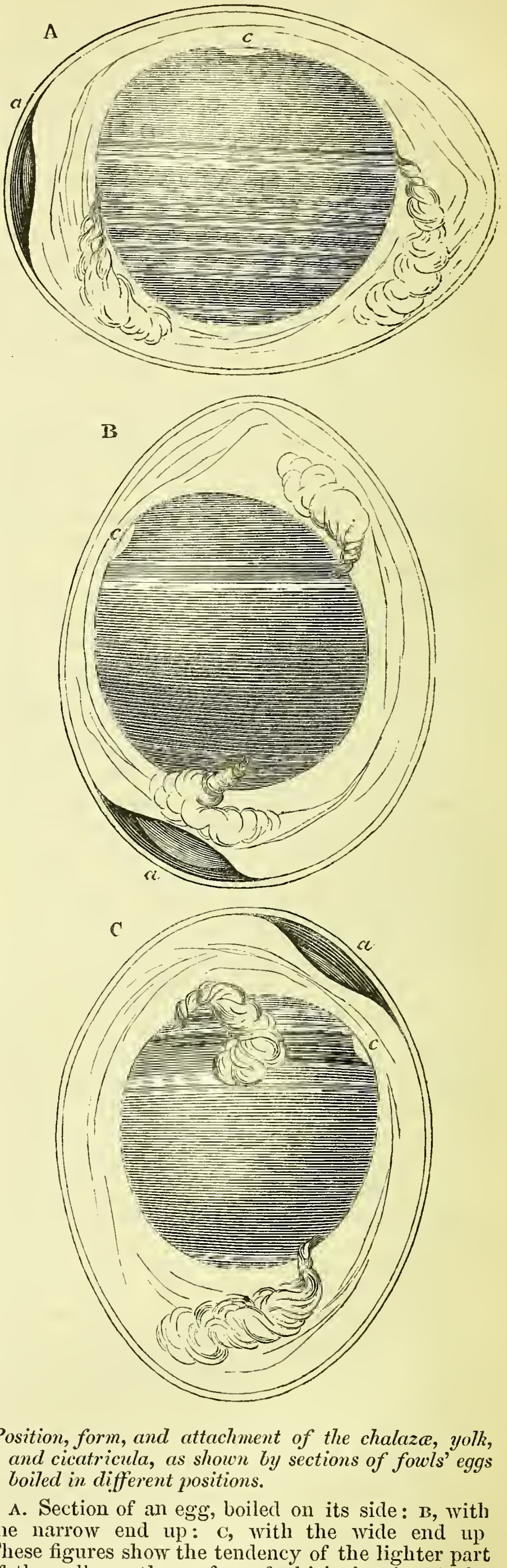
process, and in eggs that have been long kept, the space has extended over the whole width of the egg, and the quantity of gas contained in this space is sufficient to cause the eggs to float in water. The extent of the air-space may be ascertained in some degree by the greater or less feeling of coldness of the shell of the egg near the obtuse end, when it is applied to the skin of a delicate part, such as the eyelid, in consequence of the heat being less rapidly carried off by that part of the shell within which the air-space has been formed, than at others with which the albumen is in contact.

Dr. Paris found this air, amounting to about half a cubic inch, to be nearly pure atmospheric air, with a small quantity of carbonic acid towards the end of the period of incubation. MM. Baudrimont and St. Ange find it to contain in general more oxygen than atmospheric air, and no carbonic acid; whence they conclude that the shell has a peculiar power of passing outwards the carbonic acid formed during incubation and taking in oxygen.* The formation of the air-space is manifestly a compensation for the loss of substance in whatever way occasioned, that may take place from the egg. We shall have occasion afterwards to consider in how far it may be important in connection with the phenomena of incubation.

The specific gravity of the whole egg, when newly laid, and before evaporation has taken place, is generally as high as 1090, being raised considerably above the common specific gravity of the fluids and soft parts of animals by the superior density of the shell; but as the air space increases, the whole specific gravity will be lowered.

The specific gravity of the albumen and yolk differ in a considerable degree; that of the yolk, though containing the largest amount of solid matter, being lowest in consequence of the large quantity of oily matter belonging to it; and thus when the albumen becomes more fluid during incubation, the yolk naturally rises towards its upper part, or displaces some of the albumen which lay above it in the newly laid egg. It is also an interesting circumstance, that the specific gravity of the lower and upper parts of the yolk differs perceptibly; that of the upper part being reduced by the greater quantity of oily matter contained in the cells situated in the vicinity of the cicatricula. The upturning of the side of the yolk bearing the cicatricula, which is familiarly known, has long excited attention; and several explanations have been suggested of its cause; and, among others, the chalazæ have been supposed to balance the yolk in such a manner as to secure this position. But Von Baer showed that this view was erroneous, and that the less specific gravity of the upper part, or of that portion of the yolk in which the cicatricula is placed, is the true cause of the phenomenon. The measurements of the specific gravity of different parts of the egg by Messrs.

Fig. 44.



Position, form, and attachment of the chalazæ, yolk, and cicatricula, as shown by sections of fowls' eggs boiled in different positions.

A. Section of an egg, boiled on its side: B, with the narrow end up: C, with the wide end up These figures show the tendency of the lighter part of the yolk, on the surface of which the cicatricula, *c*, is situated, to be buoyed up and to expand in the white, at the same time that the movements of the yolk are to a certain extent limited by the attachment of the chalazæ; *a*, air-space.

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* Recherches Anat. et Physiol. sur l'Œuf des Vertebrés, Mém. Couronn.; published in Mém. des Savans Etrangers de l'Acad. Fran. 1850.

Baudrimont and St. Ange* are quite confirmatory of this view. They are as follows:—

Sp. gr. of the External albumen	1041·
" Internal albumen	1042·5
" Whole yolk	1029·5
" Upper part of yolk	1027·
" Lower part of yolk	1031·5†

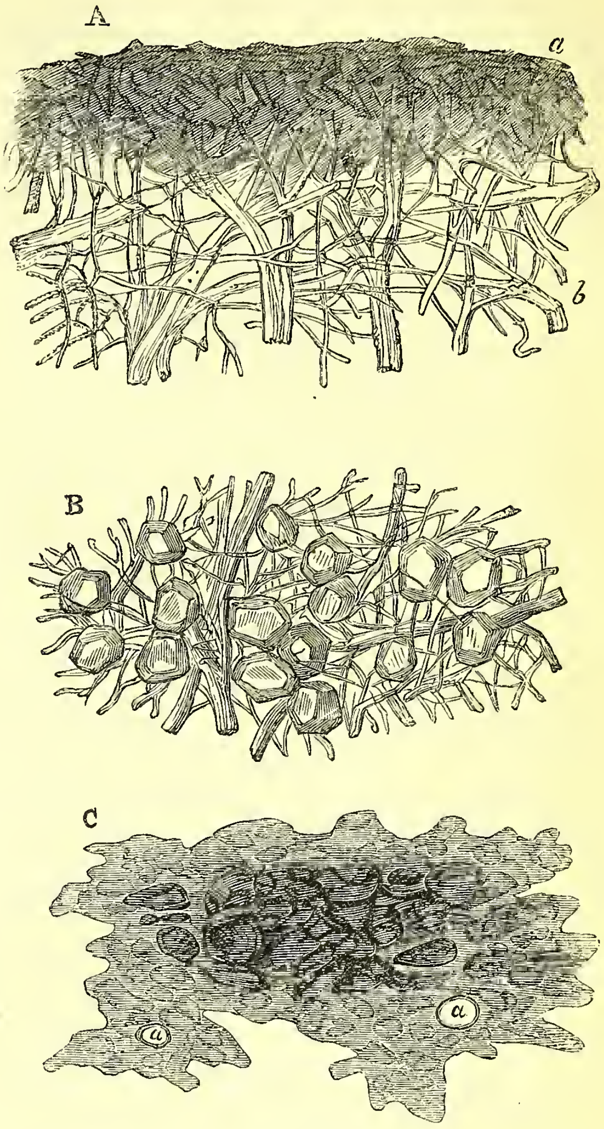
The chalazæ, being of greater specific gravity than even the inner layer of white, always float lowest; but, being attached to the yolk near its poles, they hang down from these points. All these circumstances may be illustrated very clearly by sections of eggs that have been boiled in different fixed positions, as on the side, on the large and small end; in which it will be found that, while the chalazæ exercise a certain control over the position of the yolk, that portion of its surface containing the cicatricula rises higher and expands more fully within the white than the opposite portion, while the chalazæ gravitate towards the lower side. (*See fig.* 44.)

Structure of the external parts of the egg.—The shell of the bird's egg is composed of a delicate basis of organised animal matter impregnated with the calcareous and earthy particles, the arrangement of which approaches to a crystalline appearance, but is probably of a different nature. This substance is porous, like concreted gypsum-plaster, and allows of evaporation and the mutual diffusion of gases through it in the same manner as that substance; while, by its strength and rigidity, it affords protection and support to the softer parts of the egg during incubation. The pores of the egg-shell may be easily stopped by any greasy or oily matter, or by melted wax or varnish; and then all passage of moisture or air through the shell being prevented, the development of the embryo becomes impossible. Eggs that have been oiled cannot, it is well known, be hatched; but eggs may be kept for a considerable time—weeks, or even for months—by immersion in lime-water, which impedes the evaporation and the access of air, which might favour putrefaction, while the natural condition of the contents is thus preserved.

The shell in most eggs is slightly dimpled externally, with small depressions visible to the naked eye; but these are not the openings of the pores through which evaporation or exchange of gases takes place—these being much more minute and numerous—but merely the indication of depressions caused by the largely villous structure of that part of the oviduct (uterus) in which the calcareous shell is deposited.

On removing the earthy matter by means of a dilute acid, the animal basis remains as a slightly coherent, cellular, organised structure, the form of the small compartments in which corresponds with that of the calcareous particles of the shell (see *fig.* 45. c). The internal surface is irregular and flocculent, and adheres very closely to a different kind of membrane which lines the shell.

Fig. 45.



Structure of the shell and shell-membrane in the Fowl's egg.

A. Lining membrane of the shell; *a*, thick matted or felty portion; *b*, thin shred of the torn margin, showing the peculiar fibrous tissue of which the various layers are composed.

B. Outermost layer of the same, which is incorporated with the shell; some of the angular corpuscles of the shell lying upon the fibrous substance and firmly united with it.

C. Small portion of the calcareous shell, which has been steeped in dilute hydrochloric acid, showing the remains of opaque calcareous substance in the centre, some portions of it exhibiting a granular aspect, and round the margins the animal basis or matrix from which the calcareous matter has been dissolved, presenting an irregular granular or almost amorphous aspect. Here and there clear oval cells are seen, as at *a a*.

In those instances in which the shell of eggs is coloured, the pigment substance, of various hues, is generally deposited in cells, which are strewed uniformly or in patches over the external surface of the calcareous shell. In some other instances, however, the colour seems to be merely a uniform tinge of the outermost layer of calcareous matter.*

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* Op. cit.

† Dr. Wm. Aitken has, at my request, repeated these experiments, and has obtained results in accordance with the above statement. He found the unboiled yolk to float indifferently in any part of a saline fluid of specific gravity 1035. By boiling, the specific gravity was reduced to 1031, and in both cases the side with the cicatricula floated uppermost. The upper half, containing the cicatricula, had a specific gravity of 1030; the lower half, 1032.

The lining membrane of the shell is a peculiar fibrous, interwoven structure, deposited in laminæ of some thickness and toughness, which is readily divided by tearing into two layers over the whole surface of the egg — an outer, thicker, and denser, adhering firmly to the inner surface of the shell; and an inner, thinner, smoother, and of finer texture, which may be easily withdrawn from the outer one, and which naturally separates from it at the air-space; but both the outer and inner layers of this membrane may be torn into a number of thinner laminæ, all agreeing in their minute structure.

By microscopic examination, this membrane is found to consist of a closely-interwoven network of peculiar fibres, which are of various sizes, generally between $\frac{1}{8000}$th and $\frac{1}{3000}$th of an inch in diameter; the larger frequently branching into or giving off smaller fibres at acute angles, the sides rendered uneven by minute projections or knots upon them (not represented in the figure); the larger fibres are of a somewhat flattened or ribband-like form. The external layer of the membrane contains the largest fibres. These fibres appear to be analogous in their chemical nature to those of the elastic yellow texture, not being soluble in strong acetic acid; but they do not coil up in the manner of the elastic tissue (see *fig.* 45. A).

The parchment-like coverings of the eggs of serpents and lizards, which have no calcareous shell, seem to be composed of a greater number of layers of the fibro-laminar texture now described.

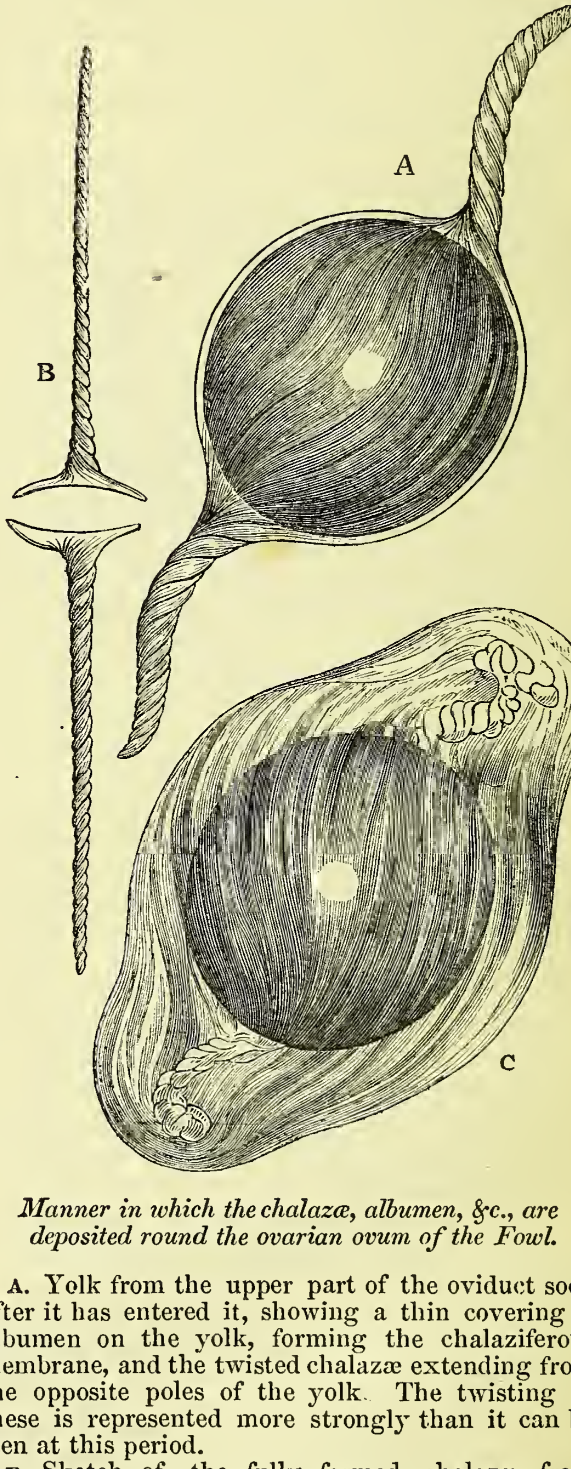
The albumen, or white of the egg, comprehends several layers of glairy, albuminous, semifluid substance deposited round the yolk, the chalazæ, or grandines, or twisted cords, and the condensed layer of albumen, forming a thin membranous investment immediately over the yolk membrane. In a perfectly-fresh egg, or in an egg taken from the oviduct previously to its being laid, the whole albumen has the consistence of a moderately-firm jelly; but very soon the outer part becomes fluid, and allows of the freer motion of the parts within the shell. This solution of the albumen proceeds to a greater extent after some hours' incubation, especially over the cicatricula.

The deeper part of the albumen, or that next the yolk, is more dense in consistence. No part of it, when unchanged by reagents, presents any sensible structure either to the naked eye or when viewed microscopically. If, however, the soft contents of a fresh egg, or one removed from the oviduct, be taken from within the shell, and thrown into water either pure or with a little acetic acid mixed with it, a slight turbidity or coagulation of the albumen takes place on the surface, which brings out the appearance of a spiral arrangement of laminæ; and in a boiled egg these laminæ may be torn in great numbers in succession from off it, the direction of the spiral being from left to right, from the large towards the small end of the egg. With a little care, almost the whole of the albumen may thus be wound off the egg in spiral strips, the deeper ones enclosing the twisted chalazæ (see *fig.* 46. D).

The coagulated albumen presents, in the microscope, a minute but indefinite granular structure.

The *chalazæ* (*grandines*) are two irregularly-twisted cords of albumen, harder than the rest,

Fig. 46.



Manner in which the chalazæ, albumen, &c., are deposited round the ovarian ovum of the Fowl.

A. Yolk from the upper part of the oviduct soon after it has entered it, showing a thin covering of albumen on the yolk, forming the chalaziferous membrane, and the twisted chalazæ extending from the opposite poles of the yolk. The twisting in these is represented more strongly than it can be seen at this period.

B. Sketch of the fully formed chalazæ from opposite sides of the yolk, stretched to their full length, and showing the opposite direction of the spiral in each.

C. Egg from above the middle of the oviduct; the first layers of albumen deposited round the yolk and chalazæ.

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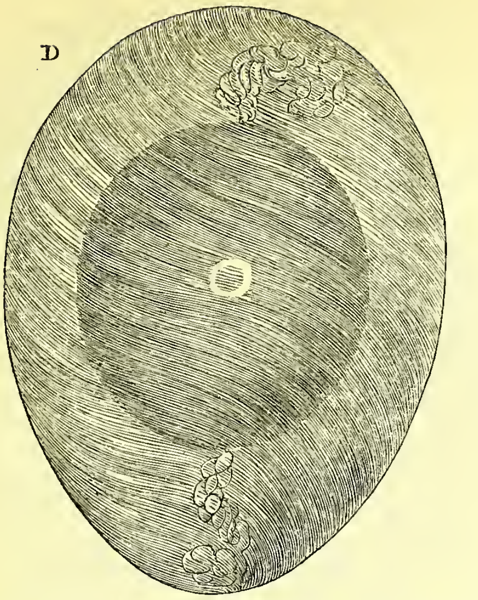
* See the works of Hewetson and others on the Eggs of Birds. Carus and Otto, Erlauterungstafeln der Vergleich. Anat. part v.



D. Egg from the lower part of the glandular oviduct near the isthmus, when the deposit of albumen is complete; the spiral arrangement of the albumen made manifest by slight coagulation.

attached to the opposite ends or poles of the yolk by means of a membrane which looks exactly like a continuation of the twisted part of these bodies opening or expanded over the surface of the vitelline membrane. These bodies attracted considerable notice from the earlier observers of the structure of the egg, and have had various uses attributed to them; but, if we may judge from the varieties they are subject to in the fowl and other birds, and their absence in the ova of scaly reptiles (otherwise very similar to those of birds), it would appear that they are only of secondary importance.

One of the chalazæ is directed towards the larger, and the other to the smaller end of the egg, and the latter usually adheres with some firmness to the inside of the shell-membrane, while that of the large end floats more freely. In this manner the yolk moves more freely at the large than at the small end of the egg. The spiral twist is in opposite directions in the two chalazæ; a circumstance depending on the manner of their production, by the gradual deposit of albumen and the spiral motion of the yolk during its descent in the oviduct. The membrane which proceeds from the chalazæ over the surface of the yolk has been called chalaziferous; and the funnel-shaped dilatation of the chalazæ where they join the membrane, has been supposed to be the opening of a tube passing through these bodies, and serving as a conduit from the white to the yolk; but entirely without reason. The chalaziferous membrane and innermost twisted part of the chalazæ are, in fact, nothing more than the first-deposited and densest parts of the albumen; nor is any importance to be attributed to a curved line or fold of the membrane which is often seen stretching over the yolk between the adhering parts of the opposite chalazæ.

The fact of the upturning of the side of the yolk which bears the cicatricula has already been adverted to, as well as the supposition that the chalazæ may be the means of securing this position; but, although it is well ascertained that these bodies control, in various directions, the motions of the yolk, they cannot be the cause of the upturning of the cicatricula; as this is secured by the difference of specific gravity in the upper and lower parts of the yolk. The true action of the chalazæ is to limit the motions of the yolk in the long axis of the egg, and control the rotation during a certain time; but in incubation the relations of the chalazæ, white, and yolk are very soon changed; and, in the progress of these changes, the remains of the denser white are collected at the lower part of the egg. If a fresh egg be turned round on its long axis, the cicatricula will keep its position upwards for one turn or a little more, and then, by the twisting of the chalazæ, the yolk is carried completely round, and balances itself again with the cicatricula uppermost in its new position.

The accessory parts of the egg, now described, are formed round the yolk or ovarian egg during its descent through the oviduct; and as they may be regarded as only indirectly connected with the functions of the true ovulum in their relation to embryonic development, it may be best to complete their history at this place by stating what has been observed as to their formation, referring for this to the researches of Purkinje, Coste, and others, which I have confirmed in most particulars by the examination of a considerable number of fowls during the process.

Formation of the external or accessory parts of the bird's egg.—These parts are produced with much greater rapidity than those of the ovulum. Many fowls lay an egg every twenty-four hours for a part of the season, while others lay only every second day, or two or three days in succession, generally at a later hour on each successive day, and then intermit for a day; other fowls lay regularly nearly every thirty-six hours. There is probably some difference in the rapidity of the descent of the egg, or at least in the length of time it remains in particular parts of the oviduct, in these various cases; but in general the whole passage of the egg, from the time of the reception of the yolk by the infundibulum to its being laid, occupies about twenty-four hours.

If a fowl which is laying only every second day, be killed and opened from seventeen to twenty hours, or if one which is laying daily be opened from three to six hours after the last egg was deposited, one of the ovarian capsules will sometimes be found completely enveloped by the infundibulum of the oviduct, which is thus in the act of receiving the ovulum or yolk about to be discharged by the cleaving of the capsule along the stigmatic band.* The infundibulum is contracted round the neck or pedicle of the ovarian capsule, so that the whole is embraced by it with moderate firmness, and the yolk thus usually passes securely into the oviduct; but it occasionally happens that capsules burst without being so embraced, or that the process is disturbed, and the substance of the yolk falling into the abdominal cavity of the fowl either produces serious injury by peritoneal inflammation, or may be gradually removed by absorption.

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* See a later section for an account of the circumstances which influence the discharge of the ovarian ovula.

The yolk enters the infundibulum, with its long axis corresponding to that of the oviduct, consequently with the cicatricula on its side, which we shall find to be its position also in the completed egg.

The passage of the yolk through the first two-thirds of the length of the oviduct, in which part the albumen is deposited, is very rapid, scarcely occupying more than three hours, according to Coste*, before it arrives in the narrow or constricted part of a more limited extent (isthmus), in which the membrane of the shell is formed. About three hours more suffice for this process, and the ovum then enters the dilated portion, which has been called uterus, in which the substance of the shell is deposited and gradually consolidated on its surface.

The albumen begins to be deposited round the yolk, immediately upon the entrance of the latter into the oviduct; at first in a thin layer, immediately investing the yolk, which subsequently becomes condensed into the chalaziferous membrane, and in two long narrow portions extending before and behind the yolk from its poles, which portions of albumen are at first straight and simple, but afterwards become twisted and form the chalazæ. (See *fig.* 46, A.)

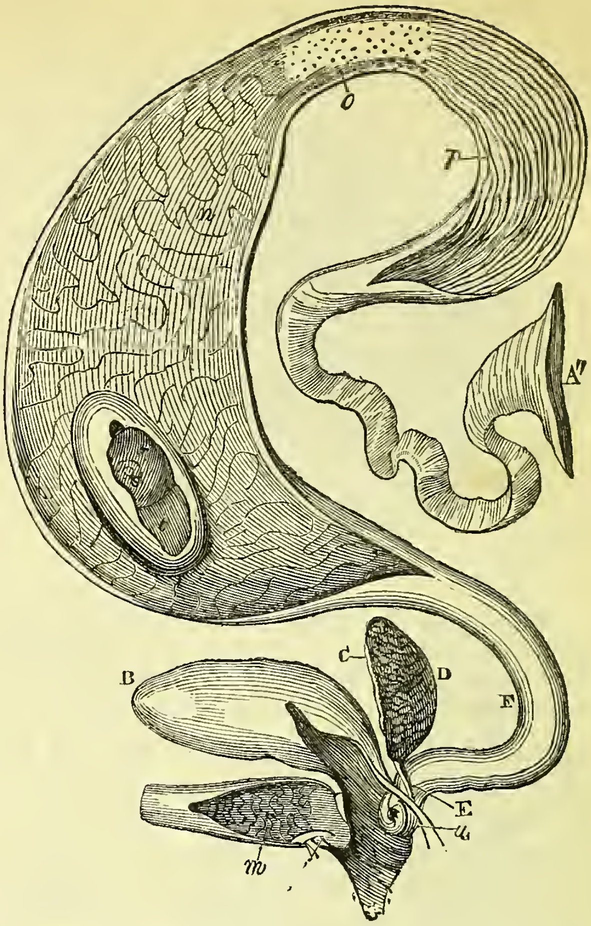
In the next part of the albuminiferous part of the oviduct, in which the glandular structure is most fully developed, the albumen is deposited in much greater quantity round the yolk and chalazæ, not following the form of the latter, and thus soon gives to the whole the oval shape which belongs to the egg; and we then recognise, previous to the formation of the shell or its lining membrane, that the narrower end of the oval is placed downwards, or advances first in the oviduct.

During the passage of the egg, and the formation of the albumen, membrane, and shell, a greatly increased determination of blood is observed in the vessels of the several parts of the oviduct. (See *fig.* 47.)

The formation of the accessory parts of the egg appears to proceed nearly in the same manner in the scaly reptiles as in birds. The accompanying figure, borrowed from the article Reptilia, is illustrative of the main features of the process.

The advancing motion of the egg of the fowl is caused by the peristaltic action of the muscular coat of the oviduct, which may be easily seen in any laying fowl opened immediately after death. The egg does not descend, however, in a straight line, but in a spiral direction, corresponding with that of the ridges of glands with which the mucous membrane of the oviduct is beset. Two peculiarities in the structure of the albuminous part of the egg result from this spiral motion — viz., the spiral laminated form of the outer layers of albumen, and the marked tortuosity of the chalazæ. It is easy to understand how the spiral form is given to the deposit of the layers of albumen. The cause of the peculiar manner in which the chalazæ are twisted is not so immediately apparent; it may be explained as follows. As already remarked, the spiral twist is in an opposite direction in the two chalazæ; one end of each of these cords must, therefore, have remained in a state of rest as compared with the other. Either, it may be supposed, the farther ends of the two chalazæ extending into the oviduct before and behind the descending yolk, remain comparatively at rest, while that body with the albumen forming round it being closely embraced by the oviduct has the rotary motion impressed upon it; or, as is more probable, when the chalazæ become attached to and involved in the deposited albumen, their outer ends move with it, while the yolk within, to which the inner ends of the chalazæ are fixed, does not rotate in the same degree; a circumstance to which it is possible the disposition of the side on which the cicatricula is placed to remain uppermost may in some degree contribute; and thus the yolk not turning so rapidly, or so often as the white, the chalazæ are twisted upon their roots attached to the surface of the yolk.*

Fig. 47.



Descent of the egg in the oviduct of the Tortoise (after Bojanus).

A. Infundibular opening of the oviduct; *n*, *o*, *p*, canal of the oviduct laid open; *s*, *t*, ovum opened, showing the yolk, albumen and shell; B, allantoid bladder; F, oviduct; C, D, kidney; E, ureter; *m*, termination of the opposite oviduct.

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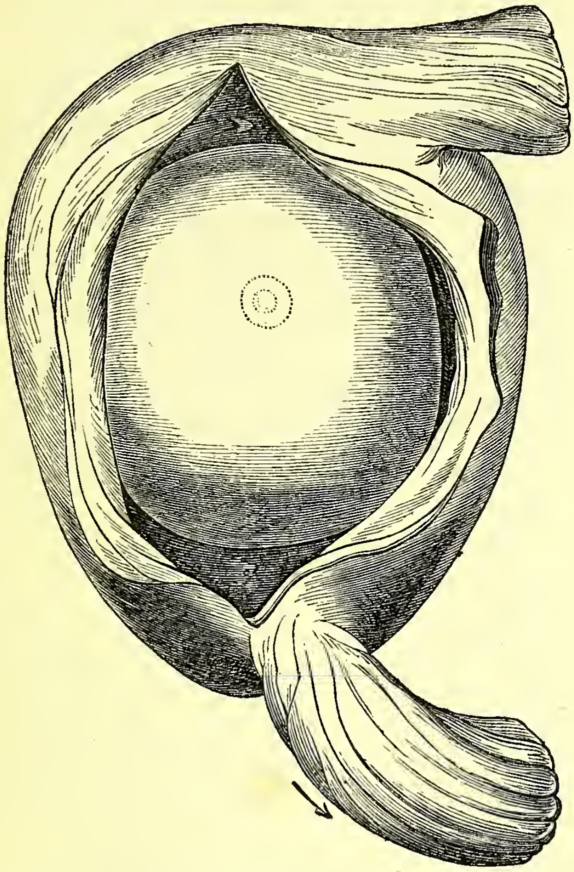
* Hist. gén. et partic. du Dével. &c.

* It ought to be observed, however, that according to Coste, the yolk does not at first rotate freely

Although it can scarcely be doubted that the chalazæ are produced during the descent of the egg, while the albumen is being deposited, it is worthy of remark, that the twisted structure of these bodies is usually not to be seen till after the shell has begun to be formed*; but it is very probable that this may depend on their not having previously acquired sufficient opacity or condensation to render their tortuous structure obvious. Indeed, Von Baer has observed them to make their appearance by increase of their opacity from exposure while under actual observation.

Fig. 48.



Position of the egg in the oviduct as it descends.

A portion of the oviduct near the lower end opened, taken from a fowl killed three and a half hours after the last egg was laid. The greater part of the albumen has been deposited, and the egg has assumed its peculiar form, the small end of the oval advancing first; the cicatricula placed on the side of the yolk.

It has been ascertained by experimental observation that the membrane of the shell is formed in the narrow part of the oviduct, termed the isthmus, which intervenes between the albuminiferous part and the uterine dilatation. It consists, no doubt, in the fibrillation of consolidated albumen, or some analogous substance, which must take place with great rapidity; but we are not yet sufficiently acquainted with the nature of this process, for the phenomena of the solidification and fibrillar organisation have not been minutely examined, nor has any difference yet been ascertained between the substance secreted in the isthmus, which undergoes the fibrillation without calcification, and that of the uterine dilatation, which seems to have no such tendency, remaining amorphous or cellular, and having very soon a deposit of calcareous matter formed in it.

By the time the egg arrives in the uterus, it has acquired its peculiar oval form, the small end pointing downwards in the oviduct. The cause of this form, which is already apparent in the white previous to the formation of the shell, is somewhat obscure, on account of the complexity of the mechanical conditions influencing the egg in its passage. It may probably depend on the circumstance that the soft mass dilates the oviduct more gradually as it insinuates itself between its coats, in being propelled onwards, while the part of the duct through which it has passed contracts more abruptly and firmly in consequence of the stimulus of distension to which it has been subjected. But the variety of forms which occurs in the eggs of different birds and other animals must not be forgotten, as indicating that the peculiarity of a lesser and greater end is not essential, and may depend on very slight or transient circumstances. Perhaps, the greater density of the albumen, secreted over the end which advances first in the oviduct, may also have some effect in giving this part the smaller volume. It certainly seems remarkable that the ends of the egg should be moulded into so smooth and rounded a surface as that of the membrane and shell by a tubular organ. In some rare instances, however, I have observed irregularities of form at the extremities of the egg, indicating an imperfect contraction of the oviduct during the passage.

The egg remains a much longer time (from twelve to eighteen or more hours) in the uterine dilatation of the oviduct during the formation of the shell. The mucous membrane of this part differs in structure considerably from the rest: it presents over its whole extent large villous-like processes, or short folds, of a flattened form, containing small follicular glands, from which the substance of the shell is secreted. As soon as the egg enters this part of the passage a thickish white fluid is poured out from the membrane, which speedily coagulates on the surface of the membrane lining the shell, and very soon we can perceive with the microscope small heaps or united groups of particles somewhat of a crystalline appearance, but in reality calcified blastema studded over the whole surface. These are the calcareous particles of the shell, which are deposited in a delicate matrix of animal tissue of a large cellular structure. The deposit goes on rapidly increasing: at first the shell is soft, it remains friable for a considerable time, and, subsequently, it

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within the white, and that it is only towards the end of the period of its passing through the oviduct that a liquefaction of the albumen, which then occurs, permits this rotation: but I think it doubtful that the adhesion between the surface of the yolk and deeper albumen is so great as to prevent the degree of rotation above referred to.

* Von Baer, Uber Entwick. p. 31.

gradually acquires the peculiar dry hardness which characterises it after the egg is laid.* The view of H. Meckel that the animal basis of the shell is formed by the separation of a layer of the mucous membrane of the uterine part of the oviduct does not appear to be established.

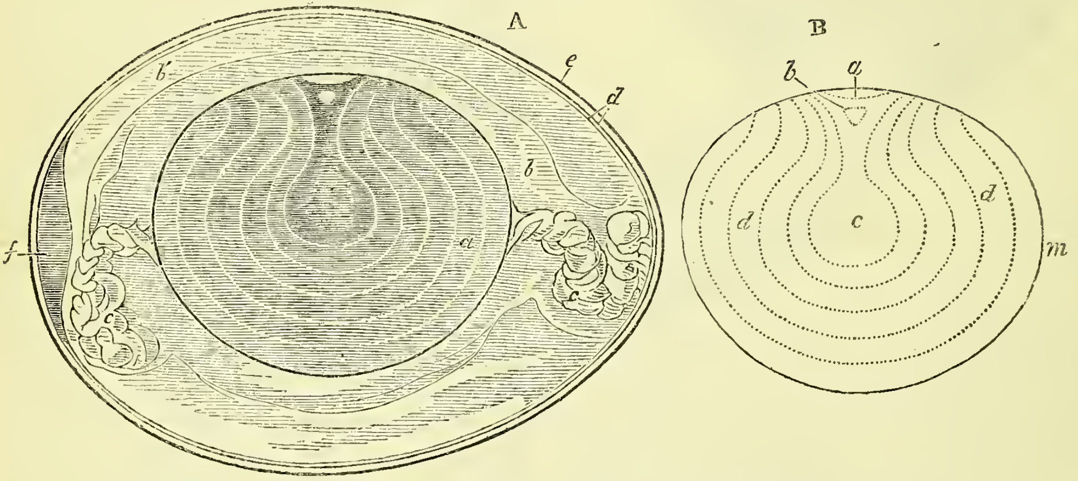
During the time that the shell is forming, the distinction between the softer and thinner external albumen, and the more dense and deeper part, becomes more obvious, and, at the same time, according to M. Coste, a certain degree of liquefaction occurs in a layer of albumen immediately surrounding the yolk, which allows the latter body to float more freely within the superincumbent albumen.

The egg remains in the uterine dilatation till it is about to be laid. The expulsion of it from this cavity through the narrow part of the tube, leading into the cloaca, requires very strong muscular contraction for its accomplishment; and, although the egg always descends in the oviduct, and usually lies in the uterus, with its narrow end downwards, both Purkinje and Von Baer state that they have sometimes seen its position inverted towards the end of the time of its residence there in consequence of the force of the muscular contractions of the wall of the oviduct.

Ovarian ovum of birds; ovulum; yolk and its contents. — The yolk, yelk, or vitellus (*Jaune*, Fr. *Dotter*, Germ.) consists in the newly laid egg of the external enclosing vitelline membrane, of the yolk substance, a mass of vesicular, cellular, and granular matter of various structure, to which as a whole the membrane gives a subglobular form, and on the surface of this mass, below or within the vitelline membrane, and on that side of the yolk which naturally turns uppermost in the complete egg, the cicatricula, or embryo spot, a thin disc of organised cellular structure, in which, under the influence of heat and air, as during ordinary incubation, the embryo, and its accompanying fœtal membranes, &c., are first formed.

The cicatricula of the laid egg, as has already been remarked, however, has, during its descent through the oviduct, undergone some part of those changes which belong to the fecundated condition, and by which the foundation is laid of that structure in which the future embryo is more immediately developed; for it has now lost its germinal vesicle, and from being formed, as at first, of mere granules or simple spherules, it has acquired a true organised cellular structure. It now consists, in fact, of the delicate discoid collection of cells, which has been called *blastoderma*. It may be proper, therefore, to consider the mass of the yolk and the germ, in their unfecundated state, while still within the ovarian capsule, next, after the ovulum has entered the oviduct, and, subsequently, when it is laid; reserving, however, for a latter part of the article the account of the process by which the change in the cicatricula referred to takes place.

Fig. 49.



Form of the Fowl's egg and structure of the yolk as exhibited by a section.

A. Sectional view of the fowl's egg; *a*, yolk enclosed by its vitelline membrane; *b*, *b'*, inner and outer parts of the albumen: *c*, *c*, chalazæ; *d*, two principal layers of the lining membrane of the shell; *e*, calcareous shell; *f*, air-space between the two layers of the shell membrane.

B. Outline of the yolk; *a*, cicatricula; *b*, nucleus of the cicatricula; *c*, yolk cavity or latebra, and canal; *d*, concentric deposits of yolk substance or halones; *m*, vitelline membrane.

In the newly laid egg the yolk forms an ellipsoidal mass, somewhat flattened on the upper or cicatricular surface, and with its long axis corresponding to that of the egg. Its largest diameter is about one inch and a quarter, its shortest about an inch: it floats within the white, capable of a certain degree of motion, which is controlled, as before explained, by its own specific gravity, and by the attachment of the chalazæ.

The yolk substance is not of the same nature throughout, there being a part of a lighter colour in the centre, about one fourth of the diameter of the whole; from this, a narrower prolongation extends upwards towards the cicatricula, near which it again widens and spreads out like a shallow cone. This whiter internal substance constitutes what has been called the central cavity (or latebra) of the yolk: the whole of this inner part has something of the shape of a flask, with a narrowing neck and a wider mouth at the top, which is, as it were, surmounted or closed in by the cicatricula. (See *fig.* 49.)

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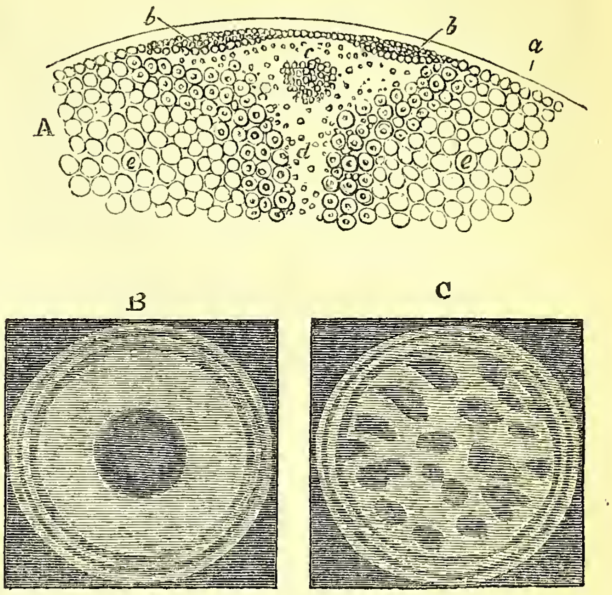
* It is to be remarked that the animal basis of the calcareous shell is of quite a different structure from the fibrous lining membrane of the shell; and the calcareous deposit is not to be regarded as taking place in that fibrous membrane. The outermost layer of the lining membrane adheres very firmly to the shell, which may have misled some on this point, who describe the animal basis of the calcareous shell as of the same structure with the fibrous lining membrane.

The shape of the yolk, I have said, is not that of a regular ellipsoid; the less density of the upper part, which is towards the cicatricula, giving rise to a widening of the yolk on that side, as may be seen in *fig.* 44, A, which represents a vertical section of an egg boiled while lying on its side. This does not depend simply on the rising of oil globules in greater quantity to the upper side of the yolk, but, as has already been noticed, on the fixed predominance of globules containing oil in the neighbourhood of the cicatricula.

Neither is the outer deeper-coloured portion of the yolk altogether uniform in structure or appearance; for it will be seen, both in the raw and boiled egg, but most easily in the latter, that several concentric layers surround the central cavity and canal of the yolk, as well as the funnel-shaped dilatation which lies below the cicatricula. These layers are marked by a slight variation in colour, and are attended by a difference in the minute structure of the corpuscles composing the alternate layers. They probably depend upon the growth of the coloured part of the yolk being more or less rapid at different successive periods.

The cicatricula of the newly laid egg is a spot of an opaque yellowish white, easily distinguished by its difference of colour from the rest of the yolk, about one sixth of an inch in diameter, and lying immediately within the vitelline membrane, in connection at its margins with the most superficial layer of the yolk substance. Examined in a favourable light* it will be found, that in the laid egg, when fecundated, the cicatricula consists of a central clearer and thinner part, and of an external more opaque annular portion. The central part is about one third the diameter of the whole, and seems as if it perforated the remainder of the disc with a circular aperture, something after the manner of the pupil of the iris. There is not, however, any perforation in reality, but only a greater thinness and transparency of the central part of the disc. Neither is this central part entirely clear; for there is placed below its middle a round heap of whitish granules, described by Pander as the *nucleus cicatriculæ* (see the figure in section), which gives greater opacity to that part when viewed directly from above. The central part of the cicatricula, already obvious when the egg is first laid, is the same which, after some hours of incubation, expands, changes its figure, and becoming still more clear, receives the name of transparent area, in the centre of which the embryo begins to be formed; while the outer more opaque part retains its greater thickness, and is converted afterwards into the vascular and peripheral part of the germinal membrane which spreads over the yolk. Round the margin of the cicatricula the deeper-coloured yolk substance is seen even in a perfectly fresh or newly laid egg to be intersected by one or more fine circles of a lighter colour. These seem to be the same which afterwards, expanding and widening, constitute the *haloes* which precede and accompany the extension of the germinal membrane over the yolk. These circles are the terminations at the surface of the concentric layers of lighter substance, which, as already mentioned, may be seen surrounding the central cavity and canal of the yolk (see *fig.* 49). It seems not improbable that, the difference in the structure of the central and peripheral parts of the cicatricula just stated proceeds from, or is connected with, the peculiar process of fissuring or segmentation which follows the disappearance of the germinal vesicle from its central part in the fecundated egg; but the description of this process belongs to a later section of the present chapter.

Fig. 50.



Structure of the cicatricula in a laid Fowl's egg.

A. Diagrammatic section of the yolk near the cicatricula, enlarged; *a*, vitelline membrane; *b*, cicatricula; *c*, nucleus; *d*, canal leading to the cavity; *e, e*, large yolk corpuscles of the coloured part: the corpuscles are not represented of their real proportional sizes, but more with a view to show their general difference.

B. Enlarged view of the cicatricula, as seen from above on the surface of the yolk in an impregnated egg: the dark central space or transparent area surrounded by an opaque zone and one or two delicate haloes.

C. Cicatricula of an unfecundated laid egg: instead of the central transparent area a number of rather irregular transparent spots are seen.

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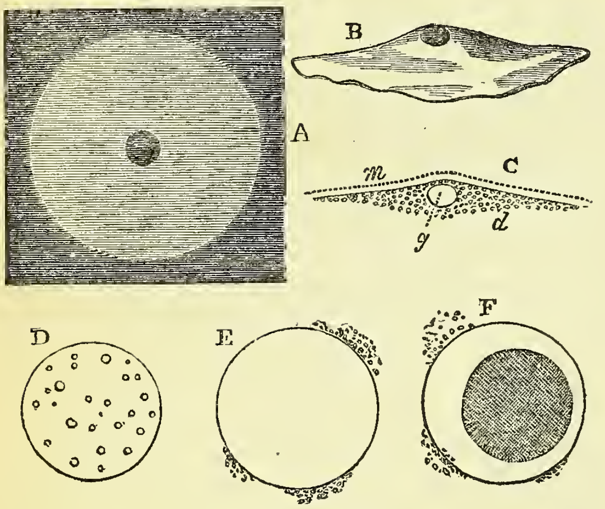
* It may be here mentioned, that by far the best mode of examining the natural appearances of the parts as they lie in the opened egg, is to allow a ray of strong or of direct sunlight to fall upon the part which it is wished to investigate, through an aperture in a screen, which places the rest of the egg and the observer in comparative darkness.

The cicatricula of the unfecundated egg, such as is laid by fowls secluded from the cock, differs from that now described principally in the absence of the marked distinction between the central clear and the peripheral opaque part. The germinal vesicle, which to all appearance remains the same in the ovary till the yolk leaves the ovarian capsule, is now no longer to be seen; and the cicatricula is often marked irregularly throughout, but more especially towards the circumference, with clearer intervals, or small irregular circular or oval spaces, mingled with the opaque substance of the disc. I have, not, however, had the means in more recent times of making a sufficiently careful examination of the cicatricula in this condition to enable me to state more minutely in what respects it differs from that of the fecundated egg.

In the ovarian yolk, while still within its capsule, a white spot corresponding to the cicatricula also exists, and occupies the same place in relation to the yolk cavity and canal. Its structure and appearance, however, are somewhat different from that of the true cicatricula of the egg which has passed through the oviduct; it is covered by a layer of closely set nucleated cells which lie below the vitelline membrane; it contains the germinal vesicle in its centre, and, instead of being thinnest towards the middle, the mass of its granular substance is accumulated in greater quantity in that part round and below the germinal vesicle, and thins gradually off towards the margin. Nevertheless, its much lighter colour than the surrounding part of the yolk makes it always easy to distinguish it. Its margin, however, is not so well marked as that of the true cicatricula; for the opaque whitish substance seems there gradually to pass into or be continuous with the most superficial layer of cells covering the yolk. To this ovarian representative of the cicatricula, Von Baer has given the name of *stratum proligerum*. It is also somewhat smaller than that of the laid egg. It is usually to be found on that part of the yolk which is next the ovary, which, as the yolk hangs within its capsule in the usual attitude of the bird, will be uppermost, and for the most part is situated close to the pedicle of the ovarian capsule. This position is not, however, a constant one; for sometimes the cicatricula is seen on the sides of the yolk, or towards the stigmatic band of the capsule, but rarely, it would appear, towards the ends or poles of the yolk.

Fig. 51.



Cicatricula, and its contents, in the ovarian egg of the Fowl.

A. A square portion of the surface of the ripe ovarian yolk, showing the vitelline disc or cicatricula, with the germinal vesicle in the centre, magnified about six diameters.

B. Lateral view of the same, to show the convexity produced by the thickness of the disc round the germinal vesicle.

C. Vertical diagrammatic section of the same; *m*, vitelline membrane; *d*, granular disc; *g*, germinal vesicle.

D, E, F. Germinal vesicles more highly magnified; D, from a yolk of about one tenth of an inch diameter, showing scattered globules or germinal spots; E, from a nearly ripe yolk, quite clear; F, from another of the same period, exhibiting a turbid or minutely granular mass from the action of water.

The cicatricula may generally be perceived on the surface of the yolk when the outermost layers of the capsule have been removed, and the germinal vesicle can be distinguished in it shining through the inner layer of the capsule and the vitelline membrane. It is placed close below the nucleated cells which line the latter, and adheres along with them somewhat to its inner surface; so that in general, it is easiest to remove this disc along with a portion of the vitelline membrane, when it is desired to obtain it for separate and more minute observation by transmitted light. The vitelline membrane being cut round with scissors at a short distance from the margin of the disc, the parts are floated off in water or serum, and then may readily be separated with a little careful manipulation.

The germinal vesicle, or vesicle of Purkinje, may always be seen with the unassisted eye, with a good light, in the centre of the ovarian cicatricula, or proligerous disc, in all ripe ovula, and in most of those which are above a tenth of an inch in diameter. It constitutes there a well-defined shaded circular spot, from $\frac{1}{80}$ to $\frac{1}{60}$ of an inch in diameter. When the proligerous disc alone has been removed for observation and laid on a flat surface, and viewed somewhat from the side, or when the granules are torn asunder with needles, so as to make a partial section of it without removing or bursting the germinal vesicle, it is easy to perceive that the middle part, containing the vesicle, is more elevated than the rest; and that, although the substance of the disc seems to pass quite smoothly or evenly from the sides over the germinal vesicle, the granules of the disc envelope the vesicle only slightly, and none cover its middle part: the vesicle, therefore, is set, as it were, in a depression of the disc, which fits round and overlaps its margins, and a considerable thickness of granular substance is continued in the disc below the vesicle. (See *fig.* 51, in section).

If we select for examination the most advanced yolk of the ovary, which, in a hen laying daily, or almost daily, would probably have been discharged from the capsule in a few hours, we may find some difficulty in isolating the vesicle of Purkinje from the granular disc; for, by this time, the vesicle has become flaccid, weak, and flattened down, and has begun to be softened and dissolved, preparatory to its complete disappearance, which generally occurs about the time when the stigma of the capsule opens to allow of the escape of the yolk into the infundibulum which embraces it. But, in all the other yolks down to those of $\frac{1}{10}$ of an inch in diameter, it is quite easy to break up the granular disc with needle points, and to preserve the vesicle uninjured. We may then free it entirely from adhering granules, and cause it to roll along in the fluid in which it is immersed, or on a plate of glass; and we may perceive that it is a simple membranous vesicle filled with fluid, and without any very obvious granules or nuclei. In the perfectly fresh state, the contents of the vesicle are almost limpid, exhibiting only a slight turbidity scarcely amounting to a granular deposit, provided it has been placed in a medium which does not change its appearance; but, if it is allowed to remain a short time in water, and still more if it is immersed in fluids which coagulate albumen, its interior speedily assumes a minutely granular aspect. The external wall of the vesicle then separates somewhat from the spherical granular mass within; and I have sometimes seen (as represented in *fig.* 51, F) a considerable condensation of the granular mass, so as to leave a large clear space between it and the external vesicle, and give it very much the appearance of the yolk mass in the ova of some small animals within the vitelline membrane. This change seems to be a combined effect of the condensation of the granular mass and the imbibition of fluid by the external vesicle. In the earlier ovula this rounded molecular mass is of proportionately smaller size; and although it differs very much from the smaller nucleus or macula contained in the germinal vesicle of the ova of many other animals, there can be little doubt that it is derived from this structure, as will appear from what is hereafter said of the progress of its development.

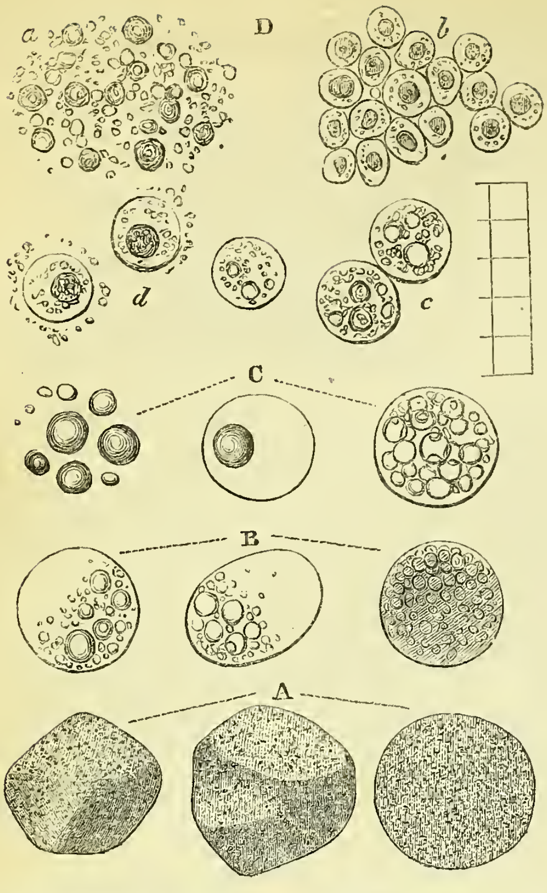
When the yolk has passed into the oviduct, and, in most instances, probably even sooner, or when it has entered the infundibulum, the germinal vesicle has entirely disappeared. Sometimes it is already gone before the opening of the ovarian capsule. The cicatricula then presents an irregularly broken appearance in consequence of the want of support from the wall of the vesicle, and the diffusion of the contents of the vesicle over the surface of the proligerous disc. The solution of the wall of the vesicle is probably a gradual process connected with the state of complete maturation of the ovule. It occurs, as is well known, in the unfecundated as well as in the fecundated egg, and cannot, therefore, in itself, be dependent on the action of the spermatozoa; neither is it altogether caused by the mechanical pressure to which the yolk is subjected in issuing from the ovarian capsule, nor by the pressure of the oviduct itself; for it usually begins, and is sometimes completed before these causes can operate.

The diffusion of the germinal substance from the vesicle (which in the fowl must have already received the spermatic influence in the ovary) has the effect thus of mingling with the remainder of the cicatricula, a material which, it can scarcely be doubted, exerts some immediate influence in inducing the change of segmentation and subsequent process of organisation by which the blastoderm is produced.

Microscopic structure of the ovum. — The investigation of the microscopic structure of the yolk is attended with considerable difficulty, in consequence both of the variety and the delicacy of the organised elements of which it consists. The following parts require our separate attention — viz., 1st. The yellow or external yolk substance; 2nd, the substance of the cavity and canal; 3rd, that of the cicatricula and cumulus; 4th, the vitelline membrane. We shall consider these both in the laid egg and in the ovarian capsule.

1. From the effect of boiling the yolk, every one is familiar with the fact that its yellow substance is coarsely granular; but the exact nature of the small bodies giving this granular structure has not been equally well understood. The examination of this substance with a microscope of moderate magnifying power in a newly laid egg, shows that almost all of the deeply coloured part of the yolk consists of spherical corpuscles of considerable size, so closely set together that they are mutually compressed; and thus, when the yolk has been hardened by boiling, the substance of the corpuscles being coagulated by heat, they present polyhedral forms; but when diffused in fluid in the unboiled state, they are all nearly or quite spherical. The size of these corpuscles varies between $\frac{1}{150}$ and $\frac{1}{500}$ of an inch; but the greater number of them are more near $\frac{1}{200}$ or $\frac{1}{250}$. Some have described the yolk corpuscles as floating in a fluid; and no doubt in the earlier condition of the yolk, a considerable quantity of fluid exists, but in the more advanced condition the amount of mutual compression they exert when coagulated is sufficient to show that its quantity must be very small indeed. Those who have described the yolk substance as mainly consisting of a fluid holding in suspension a quantity of extremely minute granules or molecules, together with some larger corpuscles, have probably been misled, by making an examination of the yolk when not perfectly fresh, and when the larger corpuscles have been in part broken up, and thus resolved into the granular fluid of which they consist. There is no doubt that in birds, and in all the large-yolked animals, the deeply coloured vitelline substance, which, in fact, forms the great mass af these ova, consists almost entirely of the large and usually spherical corpuscles just now noticed. In some animals the form is not

Fig. 52.



Microscopic structure of the elements of the yolk and ovarian ovum of the Fowl.

A. Large granular corpuscles of the yellow part of the vitellus; one of them quite spherical, as they are seen when free; two others angular from mutual compression, from a boiled yolk.

B. Various corpuscles found on the confines of the yellow yolk and the cavity and canal, showing transition forms to the next set.

C. Clear vesicles containing oil globules and detached oil globules of various sizes from the cavity and canal.

D. From the cicatricula; *a*, various-sized granules and globules forming the vitelline disc of the yolk before its discharge from the ovary; *b*, the organised nucleated cells forming the upper layer of the cicatricula in a laid egg; *c*, larger cells of the lower layer; *d*, cells of the cicatricula from an egg in its descent through the oviduct in process of formation. A scale with divisions of $\frac{1}{1000}$ of an inch is appended.

spherical; as, for example, in the cartilaginous fishes, in which a remarkable variety occurs of a cubical form, and sometimes these mixed with tetrahedral forms, as in the skate.*

When free, these corpuscles in the yolk of the bird's egg roll easily on the surface of a plate of glass as perfectly distinct spherical bodies. They present (see *fig.* 52, A) a minutely molecular or granular aspect, but with quite a smooth outline or margin to the whole corpuscle. If subjected to pressure, or cautiously ruptured with needle points, they break readily at one or more places, and allow the escape from their interior of the thick granular fluid, which flows slowly out of them in a stream. The granules are in large quantity, as compared with the fluid in which they are suspended, and are most of them of an extremely minute size, probably below $\frac{1}{30000}$ of an inch in diameter.

Although the yolk corpuscles present the distinct external margin now mentioned, and thus constitute capsules containing the granular fluid, yet we cannot, in most instances, detect any vesicular membranous envelope surrounding them. One may sometimes observe a delicate limiting line; but it has been impossible for me to determine whether it consisted really of a membrane or of a thin condensed layer of the granular substance or plasma containing it. At an earlier period it is probable that these corpuscles have membranous envelopes, but when fully formed the greater number are certainly destitute of them; for occasionally a larger corpuscle may be observed to divide into smaller ones, the outlines of which are nearly as distinct as that of the larger corpuscles.

Nor is any nucleus in general to be perceived in these corpuscles. I have occasionally seen in those from which the granular matter was escaping, and which had thus become less opaque than usual, a slight appearance of a clear hyaline circular space, but it scarcely deserved the name of nucleus; and if these spherical bodies are to be regarded as cells, which I think they ought, it must be in a somewhat different acceptation from that in which the term cell has hitherto been generally applied to vesicular organised structures. But recent researches on the early condition of cells seem to have rendered it necessary that we should include under this denomination several simple spherical minute forms of organised or organising matter, which were not at first regarded as true cells by the authors of the cellular view of organic structure; and when we consider the mode of their formation, it is more than probable that the vitelline corpuscles now under consideration may be included among the number.*

They probably constitute, at all events, as Schwann has first shown, one stage of development of a cellular structure; and, in the meantime, they may with propriety be styled the larger granular yolk corpuscles.

There is considerable uniformity in the appearance and structure of these corpuscles in nearly the whole of the deeper-coloured portion of the yolk; but immediately below the vitelline membrane, several layers of them are of a smaller size, and the outermost layer of all consists of cells which are much smaller and more compressed, distinctly nucleated and of a short cylindrical or prismatic shape. In some places also, corresponding to the concentric lighter lines which run through the yellow yolk, some approach is seen to the next kind of yolk cells or corpuscles, which I shall have to describe—viz., those of the cavity.

The substance of the yolk-cavity and canal, which in the unboiled egg may be distinguished from the other part by its lighter colour, and in the boiled egg by its softer consistence and less granular appearance, is found by microscopic examination to consist of organised corpuscles floating in a larger portion of fluid, and different from those of the external part of the yolk. The transition from the one kind of corpuscles to the other in these two portions of the yolk, is not sudden ; but many gradations of intermediate forms are to be met with on the confines of the two regions.

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* See Müller's Physiology, vol. ii.

* The above observation has a general application to such minute spherical masses of matter as are destitute of external envelope or nucleus: but in reference to the corpuscles of the yolk, I ought to observe that Schwann regarded them as cells in various stages of growth.

In the central part of the cavity or latebra, which, when boiled, appears like a thick milky fluid, corpuscles very different from those of the external part are to be found (see *fig.* 52, C). They are almost all of a very regular spherical form with a delicate and clear, but distinct vesicular wall ; the interior of the vesicle is occupied by a perfectly limpid fluid, and by one or several highly refracting globules of various sizes, not exactly similar to nuclei, but rather like oil globules, floating within the cell and moving with freedom from one part of it to another. The diameter of the clear vesicles varies from $\frac{1}{700}$ to $\frac{1}{400}$ of an inch, the most being about $\frac{1}{500}$; therefore about half the size of the granular corpuscles of the yellow yolk. The internal oil globules are of very various sizes, the largest being generally about a third or a fourth of the diameter of the enclosing vesicle. Mingled with these vesicles, there are also floating in the fluid of the yolk cavity in considerable numbers, but in less quantity than the vesicles themselves, a set of simple highly refracting globules, exactly similar to those contained within the vesicles from which we may suppose they have been set free. These oil-like globules are of every variety of size, from the minutest point up to $\frac{1}{1200}$ or $\frac{1}{1000}$ of an inch. Towards the surface of the yolk cavity and canal, and extending below the cicatricula, where the vitelline substance gradually passes into the darker yellow yolk, the microscope shows some mixture of and transitions between the several cells or corpuscles before described, those of the intermediate structure being in greatest numbers ; these exhibit very various gradations of deposit within them, from the finest granular particles in some, to larger and fewer oil-like globules in others. In most of these transition corpuscles a delicate vesicular wall is perceptible. In the more advanced of these transition forms, as the minute granules are in the process of uniting into larger and larger oil globules, and at last coalesce into a very few or into a single one, the condensation of the exterior layer increases to form a vesicular wall, and a separation of an albuminous fluid from the oil globules takes place within (see *fig.* 52, B). It is these vesicular globules of the cavity which, according to Reichert, are the more immediate source of additions to the germinal membrane in the course of development ; for the cavity and canal expand, as it were, at the expense of the yellow yolk, and as these inner globules increase the extension of the haloes and change of colour of the yolk in the first days of incubation spreads rapidly over its surface below the germinal vesicle.

3. *Cicatricula or proligerous disc.* — There does not appear to be any marked difference as to the minute structure of the mass of the yolk and its cavity in the newly laid egg and in the mature ovarian ovulum ; but the cicatricula undergoes a great change during the passage of the ovum through the oviduct, which is indicated in a marked manner by the difference in its microscopic structure. During this period, besides the loss of the germinal vesicle, the cicatricula has undergone the peculiar process of segmentation and cell formation, upon the details of which it is my intention to return in connection with the special history of that process in the ovum of mammalia, batrachia, and other animals. The cicatricula of the laid egg is, in fact, after having undergone this process, the organised blastoderm or germinal membrane in which, under the influence of the heat of incubation, the rudiments of the embryo take their origin. It already consists, before incubation, of two layers of organised cells, which are the indication or earliest condition of the upper or serous, and lower or mucous layers, which were described by Pander and Von Baer as taking their origin only after incubation for some hours.* (See *fig.* 52, D.)

The cells of the upper layer are about $\frac{1}{1500}$ of an inch in diameter. They are closely set and very slightly connected together in a continuous layer one cell thick, presenting a smoother upper surface next the vitelline membrane. Each cell consists of an external vesicular wall, a distinct nucleus, and some granular deposit. The nucleus is highly refracting. The cells of the lower layer are nearly double the size of the upper ones, more regularly spherical and less closely connected together. They do not in general present any single nucleus, but rather a small mass of granules and oil-like spherules within them, giving them much of the appearance, though smaller in size, of the corpuscles found between the cavity and rest of the yolk.

In the cicatricula or proligerous disc of the ovarian yolk, on the other hand, containing the germinal vesicle set in its centre, the microscope shows no truly organised cells, but only a mass of simple spherules of very various sizes, but the largest of which for the most part are less than half the diameter of the cells in the upper layer of the blastoderm of the laid egg. They are without any nucleus, and have all the appearance of simple solid spherules from $\frac{1}{3000}$ to $\frac{1}{2000}$ of an inch in diameter, of considerable refracting power, and, indeed, very similar to the nuclei of the cells in the upper blastodermic layer.

Vitelline membrane.—The condensed layer of structureless membrane which has generally received this name in the fowl's egg, and which I have hitherto regarded as corresponding with the immediate membranous investment of the yolk (zona pellucida) in mammalia, and in all animals, constitutes, both in the mature ovarian yolk and in the laid egg, an entire thin transparent covering of the yolk substance, without any aperture that has been discovered in it at any time; delicate and easily torn, but yet of such consistence that under water any portion of it may easily be removed and examined. In the egg which has passed through the oviduct, the vitelline membrane floats free from the cicatricula and surface of the yolk substance; but, so long as it remains in the ovarian capsule, these parts cohere somewhat together; so that, in general, on removing a part of the yolk membrane, a more or less complete lining of the nucleated or outermost layer of yolk cells comes away with it. The microscopic examination of this membrane in the fully formed yolk does not, as already stated, show any very distinct structure beyond an obscure fibrillar and molecular marking, of such fineness, indeed, as to require a high magnifying power (500 to 600 diameters) to bring it into view; and in many parts the membrane appears perfectly homogeneous. In the earlier stages of the yolk's growth, however, we shall see that this membrane is not to be distinguished from the layer of closely set nucleated cells, the outermost part of which appears to become fused together into the membrane as the yolks advance to maturity (see *fig.* 53, K *vm*). We shall presently see that the vesicular envelope which is generally termed the yolk membrane in the bird's egg, and in the ova of all animals possessing the large yolks, is probably a different *structure* from the perfectly homogeneous vesicle which in many other animals arises at a much earlier period of the growth of the ovule, and remains in them as the external covering of the yolk to the end.

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* The most exact descriptions of the minute structure of the cicatricula are those of Schwann in his Microscopic Researches; of Reichert, in his Beiträge zur heutige Entwickelungsgeschichte, &c.; and Remak, in his Beiträge zur Entwick. des Hühnchens, &c., 1850.

Early condition and first formation of the ovarian ovum in birds.—It has already been stated that the ovula exist at a very early period of life in the female bird; constituting in their earliest undeveloped condition minute cells closely surrounded by the simple vesicular capsules and the solid substance of the ovary, which at this period has not lost its primitive compact form. As the bird approaches maturity, a considerable number of the ovula situated nearest the surface increasing in size make an advance in their structure by undergoing certain changes which will immediately be more particularly adverted to. Having attained various sizes from $\frac{1}{20}$ to $\frac{1}{6}$ of an inch, they project slightly as rounded bodies from the surface of the ovary, and remain in this condition till the approach of the breeding season, when some of them destined to reach their full state of development, are at last discharged from their ovarian capsules. A much greater number, however, must remain in the undeveloped condition, awaiting future seasons of evolution; and a very considerable proportion of the whole germs of the ovary rather pass through a retrograde process and gradually disappear without having attained to any considerable size.

Of the smaller or undeveloped ova, such as those of less than $\frac{1}{10}$ of an inch in diameter, some are of a dull whitish or milky colour, the deeper-coloured external yolk substance not having been yet formed, and the yolk substance consisting almost entirely of small spherules or globules, not of true cells or of the granular corpuscles which appear at a later stage. Those between $\frac{1}{10}$ and $\frac{1}{4}$ of an inch are for the most part of a lighter yellow than the larger ovula; but above the latter size the colour has attained nearly its full intensity from the deposit externally of the deep-coloured yolk substance.

In all the ovula above $\frac{1}{10}$ of an inch it is easy to see the germinal vesicle situated on the surface of the yolk, when the capsule is opened, embedded in a more opaque and compact layer of substance which represents the discus proligerus, extending at this period nearly over the whole surface of the yolk. But in those less than $\frac{1}{15}$ or $\frac{1}{20}$ of an inch, the vesicle is not to be seen on the surface. On carefully opening or breaking up the substance of the yolk, the vesicle is easily found in the softer internal substance which flows out from the centre. From the central part of the small ovule, the vesicle appears gradually to pass outwards towards a determinate part of the surface, making its way through the proligerous layer or primitive yolk granules; and thus, in examining ovula at this stage, I have been able to perceive occasionally that the vesicle was situated in a more or less deep depression on the inner surface of that layer, which therefore must be perforated, as it were, by the vesicle in its passage towards the surface. The substance of the disc afterwards collects round the vesicle internally, and is accumulated in greater quantity (cumulus) in that situation. This change of place of the germinal vesicle from the centre or interior to the surface of the yolk in the progress of development of the ovula occurs in some degree throughout the animal kingdom; but it is especially remarkable in the eggs of birds and other animals with large yolks, in consequence of the peculiar connection of the vesicle with the proligerous disc. In the batrachia also, the change is very obvious, and the progress of the vesicle outwards has been well described by Von Baer and others. In this latter class of animals the proligerous layer covers a much greater part, or indeed in most of them nearly the whole of the yolk; but the germinal vesicle occupies always a determinate place in the centre of the layer; showing that the development of the various parts of the ovum proceeds from the first with a fixed relation of position between the germinal vesicle and other parts.

In birds, as in all other animals, the germinal vesicle, which we shall see is the fundamental part of the ovum, is proportionally large in the earlier stage of growth of the ovule, being at the first from a fourth to a half of the diameter of the whole ovule. In the progress of growth, it enlarges somewhat, but only in the earlier periods, and in less proportion than the yolk, and undergoes no farther increase during the greater part of the time that the yolk acquires the greatest addition of new matter. It is worthy of remark, however, that the germinal vesicle is originally of a large size in the eggs of birds and other large-yolked ova; that it is also of very considerable size, even proportionally larger, in the batrachia; and that in mammalia, and other animals with the smaller and granular yolk, its size bears in general a proportion to that of the yolk.

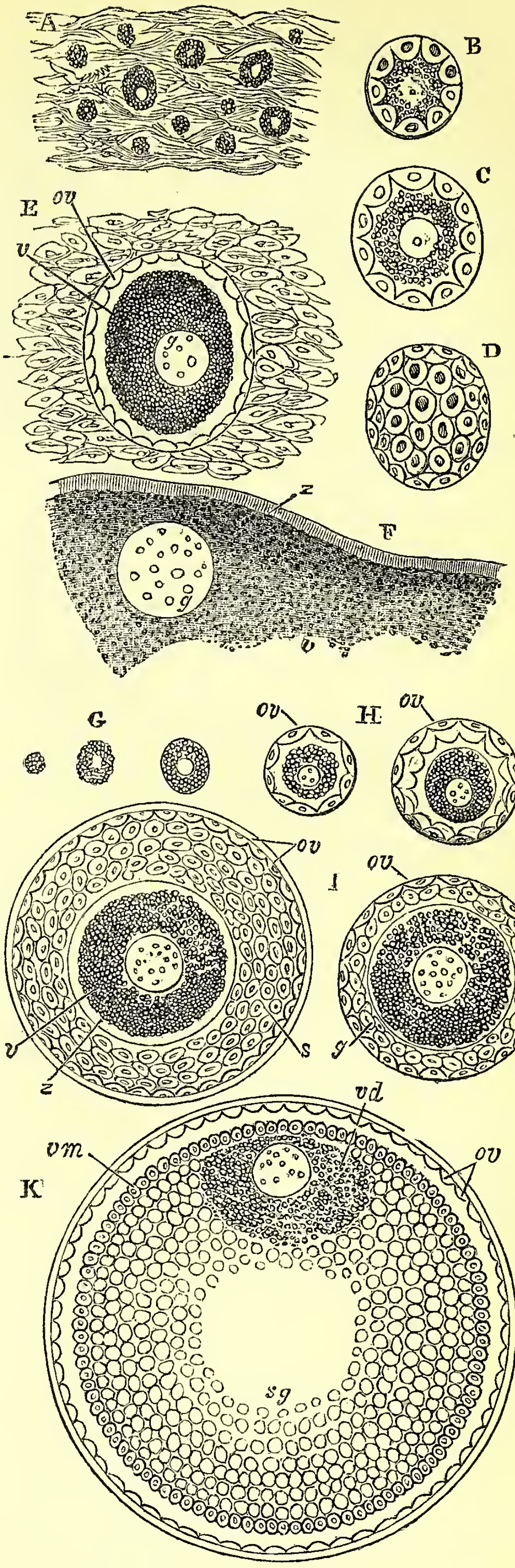
The substance of the yolk appears, in the first place, to be simply granular, or to be composed entirely of minute molecules such as those which always form the yolk in mammalia. These are united together by a somewhat glairy fluid; larger spherules gradually appear among them; and next the distinction between the substance of the proligerous disc and of the yolk cavity becomes apparent. Lastly, the deep-coloured yolk corpuscles are produced, layer after layer being deposited from the exterior, so that the outermost are the last formed. Externally a closer-set layer of nucleated cells covers the surface, in connection with which the vitelline membrane is formed.

The vitelline membrane is not formed at an early period in the bird's egg: it cannot indeed be perceived in ovula of a tenth of an inch in diameter. We shall presently see that its relations and mode of formation are peculiar in the bird's egg.

Morphology of the bird's egg as ascertained from its first origin and development. — The ovaries of the common fowl, and indeed of most large birds, are less favourable for the investigation of the first origin and earliest condition of the ovule, than those of the smaller tribes; this arises, not so much from the dense structure of the ovary in the undeveloped state, as from the great opacity produced in the ovules themselves, almost from the first, by the deposit of thick-set yolk granules. In some of the smaller singing birds, the thrush, yellow-hammer, or chaffinch, the parts are clearer and more transparent; and it will be found that the phenomena of earliest formation are most easily investigated in them.

According to Dr. Martin Barry's observations, in birds as well as in other animals, the germinal vesicle is the part of the ovum which is first formed. In the pigeon and common fowl, he has observed these vesicles in the ovarian substance at a very early period*; and he believes their origin as simple cells to precede that of the ovarian vesicles, or follicles, or, as he has termed them, ovisacs, which surround them at a somewhat later period, but still in the earliest stages of the formative process. By other observers the ovarian vesicles have

Fig. 53.



Earliest stages of the formation of the ovarian egg in the Bird.

A, B, C, D, E, F, actual representations of portions of the ovarian stroma and ovisacs of the thrush; G, H, I, K, diagrammatic sections of the same. A. In the ovarian stroma are seen the earliest state of the ova and ovisacs that can be perceived, consisting, first, of minute granular spots; next, of clear points within a minute granular mass; and third, of small germinal vesicles, surrounded with the minutely granular dark yolk substance. Compare with G, in the diagrammatic figure.

B and C. Different stages of formation of the ovisac round the small ova: the epithelium is seen to line the sac: the germinal vesicle with occasionally a single macula is now apparent. D. The epithelium of the ovisac shown in focus over the whole surface: in the other figures it is only shown in focus at the margin. E. The ovisac and ovum more advanced; *o*, *v*, ovisac, with epithelial lining; *v*, minutely granular yolk; *g*, germinal vesicle.

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* See Philos. Trans. for 1838, p. 309. In this, coinciding with the opinion previously expressed by Von Baer.

F. Part of an ovule of $\frac{1}{40}$ of an inch in diameter highly magnified: *v*, minutely granular or primitive yolk substance; *g*, germinal vesicle; *z*, thick consolidated membranous layer which formed a vesicular covering for the primitive ovule, and which corresponds to the zona pellucida of the mammiferous ovule.

I and K are intended to illustrate, diagrammatically, the view, that after the disappearance of the zona, and the formation of larger granular yolk cells, the outer layer of the cells of this substance forms the permanent vitelline membrane of the bird's egg; *v*, *d*, remains of minutely granular yolk, forming the vitelline disc round the germinal vesicle; *s*, *g*, large corpuscles of the yolk; *v*, *m*, outer layer of the cells of the same, on which the vitelline membrane is afterwards formed.

been looked upon as the primitive or first-formed structures connected with the origin of the ova, the germinal vesicles subsequently making their appearance within them. We shall return to this point hereafter in connection with the history of the mammiferous ovum. My own observations agree with those of Barry, as I have sometimes observed very small germ-vesicles or cells in the ovarian stroma without any follicular covering. But it must be admitted, at the same time, that in birds the ovisac or ovarian vesicle is formed so early that it is observed almost always coexisting with the germinal vesicle or rudiments of the ovule; so that, if the latter takes the precedence of the ovisac, it must be by a very short period.

According to Barry, there is seen almost from the first, in the clear germinal vesicle, a minute distinct granule or round spot, which constitutes the first state of the macula germinativa. Very soon the vesicle is surrounded by a small quantity of a clear fluid in which are rapidly deposited globules or granules constituting the first rudiments of yolk substance. There is no vitelline membrane, however, in birds, at the first; nor are the larger cells which at a later period intervene between the ovisac and the primitive yolk, formed in the earliest stage. The smallest ovisacs which Barry observed, and which consisted of perfectly simple vesicular linings of the cavities containing the rudimentary ova, in the pigeon and common fowl, were from $\frac{1}{600}$ to $\frac{1}{300}$ of an inch in diameter.* At a somewhat later period, the number of maculæ (nuclei) in the vesicle, and of the yolk granules externally, had increased, and a delicate membrane, which he describes as vitelline membrane, and believed apparently to be the same which afterwards surrounds the large yolk in the fully-developed ovum, has made its appearance. At this period also there begin to be formed within the ovisac a set of larger nucleated corpuscles or cells, which are external to the true ovum, and which may be considered as corresponding with the so-called granular contents (substantia and tunica granulosa) of the Graafian follicle in mammalia.

The early structure and development of the ovum of birds have more recently been described, with considerable detail, from observations on the chaffinch and common fowl by Dr. H. Meckel*; and as the observations of this author have led him to take a somewhat different view of the relations of some of the parts of the ova of birds and other animals from that which has hitherto been generally adopted, it will be proper to give a particular account of them in this place. Many physiologists have felt the incongruity of the comparison generally made between the minute and simple ovum of the mammifer, and the large and more complex yolk of the bird, and most are disposed to acknowledge the necessity of making some more marked distinction between the granular and the cellular yolk substance in the two great groups to which these ova respectively belong. It has before been stated, that Von Baer on his discovery of the mammiferous ovum, regarded it as corresponding, not to the whole ovum of birds, but to the vesicle of Purkinje. The discovery, in 1834, of the germinal vesicle in the mammiferous ovum, of the existence of which Von Baer had no distinct knowledge, induced Valentin and others to maintain that the essential parts of the ovum are the same in the bird and the mammifer. But it may be doubted whether physiologists may not have proceeded further than they were warranted by observation in regarding the vitelline membrane and large corpuscles of the yellow yolk of birds as essentially corresponding parts with the zona pellucida and the smaller granular yolk of the mammifer. For the membrana vitelli of the bird's egg may, perhaps, be more analogous to the outermost layer of the membrana granulosa of the Graafian follicle, and the large cellular yolk to a part of the same substance or the fluid of the Graafian follicle; while the minutely granular yolk in which the cicatricula originates and the germinal vesicle together are the true representatives of the small ovum of the mammifer. It seems undoubted, that what we term the yolk membrane in the fowl's egg does not exist in the early stages, and is formed indeed only as the ovarian egg approaches maturity, and it is admitted that no large cells similar to those of the bird's yolk exist within the cavity of the zona pellucida of the mammiferous ovum. If this view is correct, we may expect to find a representative in the egg of the bird and of other animals having similar ova, of the very marked enclosing vesicle, which has received the name of zona pellucida in the mammiferous ovum. Now, according to H. Meckel there is, not from the very first, but in the earlier stages of formation of the yolk of the fowl and of other birds, a homogeneous vesicular membrane enclosing the primitive or granular yolk, or what he terms the true egg substance. As the cellular yolk is formed, this membrane, to which he thinks himself warranted in giving the name of zona pellucida, disappears, and already in ova above $\frac{1}{10}$ of an inch there is no trace of it left.

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* Vide loc. cit. Plate v., figs. 18, 19, and 22 of pigeon; figs. 23 and 24 of common fowl. The membrane which Barry described as vitelline in the earliest stages of growth of the bird's egg was probably not so, but the outline merely of the albuminous substance in which the primitive yolk granules are deposited. This will be made more apparent in our description of the formation of the ova of Batrachia.

* See his paper, Die Bildung der fur partielle Fürchung bestimmten Eier der Vögel, &c., in Siebold and Kölliker's Zeitsch. für Wissenschaft. Zool. vol. iii. p. 420, 1852.

The observations of H. Meckel on this subject appear to be both novel and important; but he has not been equally successful in the theoretical deductions made from them. In the commencement of the paper before referred to, he thus announces his view of the morphology of the bird's egg: "For a right and consistent nomenclature and definition, we must designate the corresponding parts according to their analogy with those of the human body. I believe, therefore, that that alone ought to be regarded as the true egg which exists in Man, Mammalia, Naked Amphibia, and Osseous Fishes; and that in the remaining Vertebrata the ovum consists only of the so-called vesicle of Purkinje, and that all the other parts are accessory, superimposed, and unessential. In particular, that the yellow yolk of the bird and scaly reptile is analogous to the corpus luteum of the human ovary, the albumen ovi to the uterine secretion, and the calcareous shell to the decidual mucous membrane of the uterus." Von Baer, at p. 32. of his Epistola, uses the following words, which have been much controverted by some of those coming after him, but which show that he was aware of the difference in the relation of parts in the birds and mammiferous ovum: "Vesicula ergo Graafiana cum ad ovarium generatimque ad corpus maternum respiciamus, ovum sane est Mammalium, sed evolutionem quod attinet, vehementer discrepat a reliquorum ovo animalium," &c. And again, "In mammalibus vesicula innata vitellum magis exultum continet, et ratione ad fetum geniturum habita verum sese probat ovum. Ovum fetale dici potest in ovo materno. Mammalia ergo habent ovum in ovo; aut, si hac dicendi formula uti licet, ovum in secunda potentia." Both in the Epistola, and the Commentary upon it, Von Baer insists strongly on the analogy between the cellular substance of the Graafian follicle and the yellow yolk; and he seems to have erred chiefly in limiting his comparison of the mammiferous ovum (within the zona) to the vesicle of Purkinje of the bird's egg. If, therefore, we modify Von Baer's view so much as to regard the vesicle of Purkinje along with the granular cicatricula of the bird's egg, as corresponding to the whole of the mammiferous ovum, and the granular cells (tunica granulosa, &c.) of the Graafian vesicle as corresponding to the yellow yolk (the zona pellucida having disappeared in the bird's egg), we shall establish a more correct relation of the parts than that suggested by H. Meckel. I am not aware of any animal in which the germinal vesicle alone, without some yolk substance and an external inclosing membrane (zona, or vitelline membrane) forms the entire ovum.

I will now state the result of my own observations on this subject, by which I conceive is proved the correctness of H. Meckel's view, that in birds there is a primitive ovum, enclosed within a zona, distinct from the large mass of cellular yolk, which is formed at a later period.

As soon as the membranous wall of the ovisac or ovarian follicle has become distinct in the ovary of the fowl, we can perceive at the same time a layer of larger cells lining it which form a clearer ring round the opaque ovule. The ovule itself consists then merely of the germinal vesicle and a small quantity of the primitive yolk substance. The latter becomes opaque at so early a period that it in general hides completely the germinal vesicle. It seems to arise by the deposit of very fine granules, probably of an oily nature, in a dense albuminous fluid or blastema which collects round the germinal vesicle very soon after the latter is invested by the ovarian follicle. In follicles of $\frac{1}{100}$ of an inch in diameter the primitive ovule, the membrane of the enclosing follicle, and between them the layer of larger clearer cells, are all perceived with facility. There is not yet, however, any investment of the ovule comparable either to a zona pellucida or vitelline membrane.

In ovarian follicles of $\frac{1}{30}$ or $\frac{1}{40}$ of an inch in diameter, a farther progress is to be perceived. On bursting any such follicle with fine needle points, the ovum is ruptured, and the germinal vesicle usually first escapes along with the more fluid internal part of the yolk, in which it is freely suspended. This vesicle is about $\frac{1}{130}$ of an inch in diameter, presenting externally a smooth, thin and delicate vesicular membrane of a spherical form, of which the double outline is just discernible with a magnifying power of 300 diameters. The vesicle is partly filled with fluid and partly with a finely granular spherical mass of no great opacity, which corresponds to the macula germinativa. In most instances this mass occupies about two thirds of the diameter of the vesicle. The yolk substance, which has scarcely altered from its primitive opaque finely granular condition, now consists of a more fluid internal part containing fewer granules, and in which the germinal vesicle floats, and of a more consistent external part. In the latter a manifest change has occurred in this respect, that towards the outer surface there is separated a much clearer ring of substance contrasting strongly with the more opaque part. This may with correctness, it is true, be described as a membrane, as H. Meckel has done in comparing it with and giving it the designation of the zona pellucida. But the very remarkable structure, which the author now mentioned has had the merit of first pointing out, is one deserving of the greatest attention. It has appeared to me to be gradually formed in ovula of about $\frac{1}{80}$ or $\frac{1}{60}$ of an inch in diameter, by the clearing and partial consolidation of the outermost part of the albuminous basis or blastema in which the granules of the primitive yolk substance are deposited. It is at first comparatively thin: it is most apparent by its greater clearness and consistence in ovules of $\frac{1}{40}$ or $\frac{1}{30}$ of an inch in diameter, in none of which have I ever failed to observe it. In those of $\frac{1}{20}$ it becomes broader, but less clear and somewhat softer in its consistence, and is uneven and as if softening away or breaking up on the external edge; and in ovules of $\frac{1}{10}$ of an inch it has in general disappeared. At no period have I observed it to assume the glassy transparency, nor has it the distinct outline and membranous appearance represented by H. Meckel; but it seemed rather like a portion of the albuminous basis of the yolk substance, nearly but not quite deprived of the granules, which are thickly deposited in the rest.

While these differences are stated, however, it appears to me warrantable to coincide in so far with the view of H. Meckel as to regard this structure as a temporary representation in the fowl's egg of the zona pellucida, which in the mammiferous ovum assumes greater consistence, passes into the membranous form, and constitutes the only ovarium covering of the ovule.

In ovules of $\frac{1}{30}$ to $\frac{1}{20}$ of an inch in diameter, the layer of nucleated cells placed between the primitive ovule and the membrane of the follicle, and which may be looked upon either as a cellular lining of the follicle or a peculiar investment of the ovule, has become more distinct and consistent, and the cells of the outermost layer have assumed the form of short compressed prisms. They have finely granular contents and clear nuclei, with one or sometimes two nucleoli, like the cells of the tunica granulosa of the mammalian follicle. It appears that these cells come afterwards to form the external part of the yolk of the bird's ovum, the cellular part of the yolk being formed within them, and the vitelline membrane being produced on their outer surface.

The bird's ovule, it is well known, usually fills completely the ovarian follicle; but in several instances I have observed, from imbibition of water or some other cause, the ovule to occupy not more than half the diameter of the follicle, the remainder being filled with a clear fluid; and in these instances the prismatic layer of cells adhered closely to the surface of the zona and primitive granular yolk.

In ovules of from $\frac{1}{20}$ to $\frac{1}{10}$ of an inch the formation of the vitelline membrane appears to commence. The external nucleated cell covering has increased in quantity, and adheres more closely to the granular yolk, with which it generally comes away when the follicle is opened. The external edge of the layer of prismatic cells, the length of which is considerably increased, is now surrounded by a narrow pellucid space enclosed by a double line, presenting the appearance as if a small part of the bases of these cells had been fused together in a homogenous film. This is the commencement of the formation of the true vitelline membrane, which in the latest period of ovarian growth of the ovum becomes nearly quite structureless, but which throughout the greater part of the process retains somewhat of the hexagonal marking from the close adhesion of the cells by the amalgamation of a part of which the membrane has been produced.

In follicles of about $\frac{1}{10}$ of an inch or larger the true cellular elements of the yolk have begun to be formed. The manner in which these originate I have not as yet had the means of determining with precision. They appear, as H. Meckel has suggested, to be produced as a secretion from the interior of the ovarian follicle; but they are more immediately formed within the layer of prismatic cells which envelope the whole ovule. Nor have I been able to determine their precise relation to the zona and primitive fine granular yolk. When the zona has disappeared, as is usually the case in ovules of $\frac{1}{10}$ of an inch, the cellular elements of the yolk seem to begin to mingle with the finely granular substance. At first, cells and larger oil globules, similar to those of the yolk cavity, are produced. So long as these alone exist, the yolks have a dull milky-white aspect. Later, or in those of $\frac{1}{6}$ of an inch, or even somewhat smaller, the yellow tinge appears, and this very soon becomes more decided, at the same time that the peculiar large granular corpuscles or cells are formed in which the vitelline colouring matter principally resides. These corpuscles are produced in successive layers within the layer of prismatic cells of the external tunic; and it is probable that there is some periodical variation in the rapidity of their formation from the alternation of concentric layers of deep yellow corpuscles with those of a lighter colour which may be observed in the section of a boiled yolk. The corpuscles of the yellow yolk are not, however, formed in equal quantity in every part: indeed they are quite deficient at that side on which the remains of the primitive granular yolk with the imbedded germinal vesicle are situated.

With regard to the germinal vesicle, it is to be observed that it is at first quite free in the more fluid internal part of the primitive yolk; in the next stage, before the formation of the cellular yolk, the germinal vesicle comes to be imbedded in the more consistent external part of the primitive granular yolk; and it is, no doubt, chiefly the remains of this which form the germinal or vitelline disc: but further observations are still required to determine the precise manner in which this arrangement of the primitive yolk in the discoid shape takes place.

It appears, further, that in the formation of the elements of the more advanced yolk, the earliest produced, or innermost, remain the softest; the latest formed, or outermost, acquire the greatest consistence. The external layer of prismatic cells next the vitelline membrane passes with it completely round the whole yolk and over the vitelline disc; the next layer, less prismatic and more rounded in their form, but still distinctly nucleated cells, covers the whole surface of the yolk, with the exception of the part occupied by the vitelline disc, with the margin of which this layer is continuous. The next layers passing inwards consist of granular corpuscles, which do not in general present the appearance of nucleated cells.*

In conclusion, therefore, the ovarian ovum of the bird being formed in an ovarian capsule, is at first very similar to the Graafian vesicle of the mammalia, and differs chiefly in the earliest stages from the mammiferous ovum in the proportionally large size of the germinal vesicle, and in the absence from this vesicle of the more distinct and persistent nucleus which exists in animals having the smaller yolk. This germinal vesicle may be looked upon as the fundamental part of the ovum in both kinds of animals. Along with it there exists, from a very early period in birds, a granular opaque yolk substance. This substance by itself constitutes the whole yolk of mammalia; but in birds it probably remains as a part, if not the whole, of the proligerous disc (afterwards cicatricula). The mammiferous ovum is closely surrounded at an early period with a dense transparent membrane (the zona pellucida) formed by a condensation of the outermost layer of the albuminous part of the yolk; and a similar envelope, but less dense, exists in the earlier stages of formation of the fowl's egg, surrounding the finely granular primitive yolk substance along with the germinal vesicle. In both birds and mammalia the ovarian follicle, besides being lined with a layer of epithelial cells, secretes, or has formed immediately within it, a quantity of nucleated granular cells more loosely united together, known in mammalia by the somewhat inappropriate names of tunica granulosa and substantia granulosa of the ovarian follicle. But in birds, although this substance is at first somewhat similar in structure and relations, cells afterwards increase within it in very large quantity, and acquire a peculiar structure and colour, constituting the yellow part of the yolk substance. The outer covering of the yolk, or vitelline membrane, is only produced when the ovule has attained considerable advancement, by a new deposit upon the external surface, or by the condensation of a part of the external layer of these cells, which covers the whole yolk, together with the cicatricula. The germinal vesicle is fixed in the bird's yolk, towards the surface, in the proligerous disc. In the mammiferous ovum the germinal vesicle is, for the most part, near the surface of the yolk substance, but not so far as is known in a determinate situation, and the whole ovum in its zona pellucida is fixed in the tunica granulosa towards that part of the follicle which is next the surface of the ovary.

The germinal vesicle bursts or is dissolved in both. In mammalia it is probably diffused through or over the whole granular yolk: in birds it probably overspreads only the proligerous disc. The whole yolk is segmented in mammalia, while in birds this process is confined to the proligerous disc, out of which the blastoderma is produced.

The full description now given of the structure of the bird's egg will enable me to treat comparatively briefly of that of other animals. In regard to most of them, indeed, it will scarcely be necessary to do more than to notice their most important peculiarities.

Before leaving the ova of the first group, it may be noticed on the authority of Leuckart*, that in the scaly reptiles there is not the same difference between an external coloured yolk and the lighter cavity as in birds, but that the whole yolk substance is of a paler colour, and of a more clear and uniform appearance. Still from a preponderance of oily matter in the vicinity of the cicatricula, there is the same tendency to that part of the ovum floating uppermost. The germinal vesicle in the ovarian ovum of these animals presents at an early period a very subdivided condition of the macula; and it is placed in a granular disc, which does not appear to differ essentially from that of birds. The vitelline membrane is equally structureless. Leuckart has traced the development of the ovum in Lacerta crocea and Coluber lævis, and has ascertained that in them, as in birds, the primitive yolk substance is destitute of cellular elements, and has at first no special covering. The true or external vitelline membrane is probably formed, precisely as in birds, on the exterior of the outermost layer of the cellular part of the yolk.

In the cartilaginous fishes there is a greater departure from the type of structure now described. The external vitelline membrane is of great delicacy, and is perceived only with difficulty. The yolk substance is in great part composed of peculiar angular corpuscles, sometimes flat and tabular, at other times cubical, octahedral, and of other forms. It has been stated by Leydig* that in the plagiostomatous fishes there is no vitelline disc or cicatricula; but this does not agree with my observations in the common skate fish, in the ova of which I have always observed a very distinct flat disc about three-eighths of an inch in diameter, of a lighter colour than the surrounding part of the yolk, and situated on the surface which naturally floats uppermost. The germinal vesicle, which is larger than that of birds, sometimes $\frac{1}{40}$ of an inch in diameter, is extremely delicate and very easily ruptured. Its nucleus or macula is originally single, but becomes afterwards subdivided or multiple and diffused.

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* While the above was passing through the press, I received the 27th and 28th parts of R. Wagner's Handwörterbuch der Physiologie, containing the Article "Zeugung," by Professor Leuckart of Giessen. I regret that I have not previously had the advantage of perusing the very luminous and comprehensive sketch, by that author, of the structure and morphology of the ovum of different animals. As, however, Professor Leuckart has stated that his observations do not confirm the statements of H. Meckel in regard to the zona pellucida of the bird's ovule, I have thought it right, notwithstanding the unfavourable period of the year (October), to repeat carefully my examination of this matter; and I have here to state that, in the common fowl and thrush, the description given above has received the fullest confirmation. While, therefore, I am inclined to differ, as above stated, from the views of H. Meckel as to the morphological analogy of parts of the ovum in different animals, I must admit the existence, at a certain stage, of the very peculiar structure pointed out by him, as corresponding with the zona pellucida, with the differences as to details which I have there mentioned. The primitive ovule of the bird therefore consists of the germinal vesicle, granular yolk, and this so-called zona; and the cellular substance of the bird's yolk, is the product of secretion, or is a modification of epithelial formation from the interior of the ovarian follicle.

* Art. *Zeugung.*

The ova of the cephalopoda, which may, according to most embryologists, be included in this group, are of considerable size. They possess a germinal disc, and the segmentation of the yolk is partial or is confined to that disc, as in the animals previously mentioned.† The large yolk corpuscles are spherical masses of united oil granules, and like the most of those of the bird's egg without any true enclosing vesicle. The germinal vesicle is of considerable size, and has subdivided maculæ. The whole are enveloped by a fine structureless vitelline membrane. In the course of the formation of the ovum, the external part of it undergoes a remarkable change in being folded inwards in numerous deep grooves, which almost reach the centre of the yolk. This folded structure is in the smaller species again effaced before the ova reach maturity, but in the larger species it appears to remain, and to be the cause of a peculiar reticulated marking over the surface of the ova.

In regard to other classes of the invertebrate animals of which the ova may appear to belong to this group, I shall have occasion hereafter to state some additional facts, in explanation of the manner in which in some of them the granular and cellular elements of the yolk are occasionally combined.

From the foregoing considerations, then, it appears that in ova of the first group as distinguished in this treatise, the germinal vesicle is at once the first formed and the fundamental part of the ovum around which the rest of the parts are deposited. It alone, therefore, is strictly to be regarded as a simple or primary cell. It may aptly be called the *Germ-cell*. In birds its nucleus or macula is originally simple, but at a very early period it undergoes subdivision into nucleoli or maculæ, so numerous and minute as at last scarcely to be recognisable, and thus the germinal vesicle loses in such animals somewhat the characteristic cellular structure which it presents in many others. Next, by aggregation of the primitive yolk substance round the germ-cell, and by the gradual consolidation of a clear film on the outermost part of the albuminous matrix of this substance into the form of an enclosing vesicle, there is produced the *primitive ovum*, a secondary cell, in which the zona pellucida constitutes the cell wall, the oil granules and albuminous fluid of the yolk substance the contents, and of which the germinal vesicle is now the nucleus. And lastly, if it is considered desirable to extend the application of the term cell also to the mature state of the ovarian egg of the bird, we may perhaps still regard that organism as a tertiary cell (in the ascending series) formed by the superposition of new parts, some of which are themselves cellular in their origin, round the primitive ovum, the whole being at last enclosed and moulded in the vesicular form by the external vitelline membrane; a peculiarity of this formation being that in the meantime the wall of the secondary cell or primitive ovum has disappeared. But, notwithstanding the spherical form, the isolated position, and the simple structure of the parts which compose the completed ovarian ovum of birds, doubts may fairly be entertained as to the propriety of bringing such complex organisms under the designation of cell as now generally employed.

§ 5. More detailed description of ova belonging to the second group, or with small granular yolk and complete segmentation.

If the foregoing views are correct, it appears that, while the ova of birds and other animals of the first group contain within the vitelline membrane the whole product of formation which belongs to the ovarian capsule, the ova of mammalia and animals of the second group comprehend only those parts of the contents of the Graafian follicle which are formed within it at the earliest period — viz., the germinal vesicle and the primitive yolk substance with its limiting zona. In the Graafian follicle of mammalia, there is likewise produced a large proportional quantity of cellular elements and albuminous fluid, the tunica and substantia granulosa, &c., in a part of which (cumulus proligerus), the ovum comes to be imbedded in the progress of their formation; and these superadded contents of the Graafian follicle escape along with the ovum when it leaves the ovary, but do not apparently maintain any long or constant connection with it.

In the ova of those invertebrate animals which belong to this group, the conditions of formation do not admit of their comparison with those of mammalia; but they agree with them in so far that the first germ-cell is enclosed by a finely granular yolk, and that the vesicular envelope of the ovum generally corresponds to the zona formed by consolidation on the surface of the primitive yolk.

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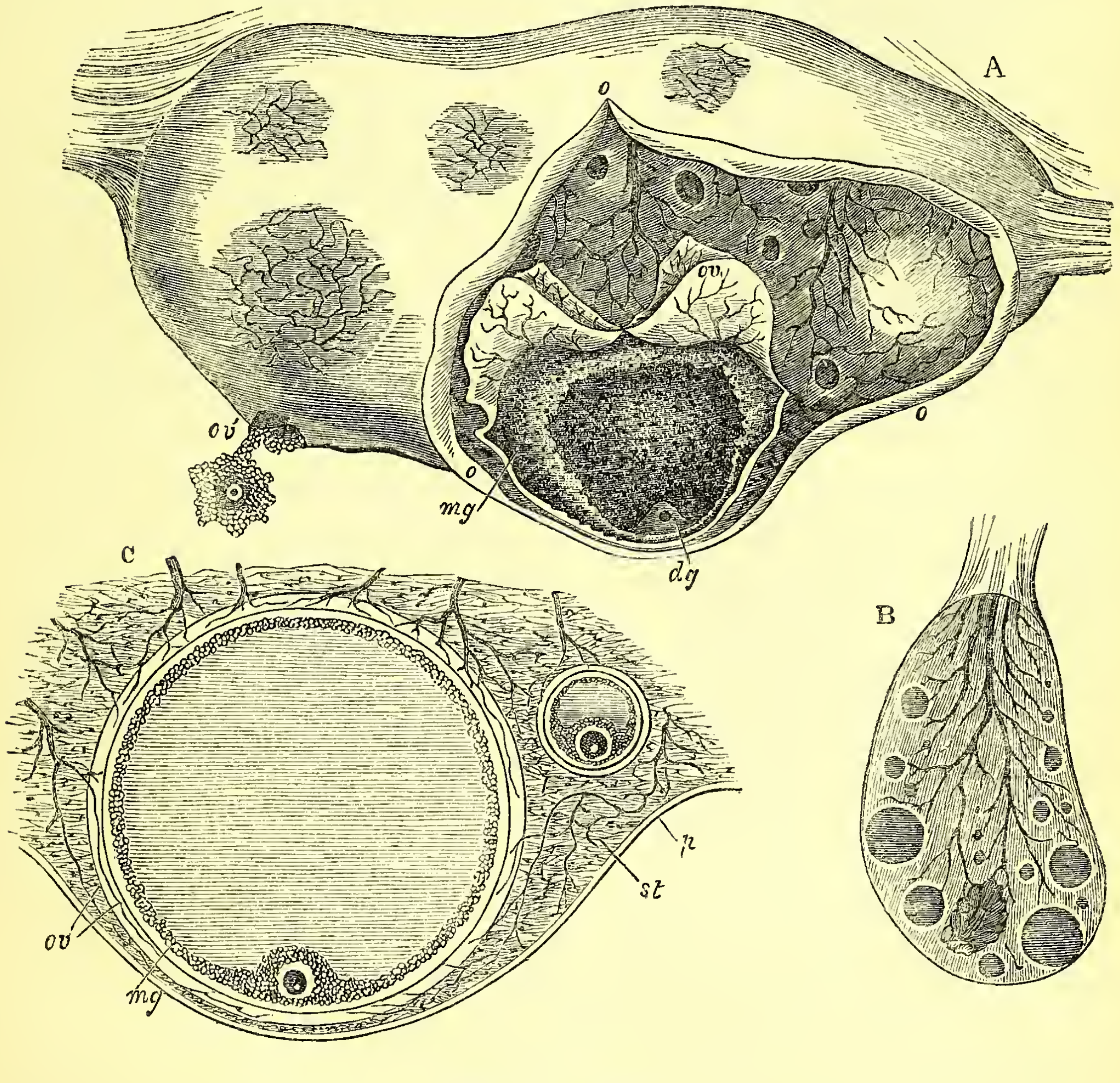
* Beitrage zur Mikroskop. Anat. der Rochen und Haïen, p. 87., a work which I quote only from Leuckart.

† We owe this interesting discovery to Kölliker. See his work on the Development of the Cephalopoda. Zürich, 1844.

Ovum of Mammalia and of the Human Species.—There is a remarkable uniformity in the size, structure, and relations of the ovarian ovum in the whole class of Mammalia, with the exception of the families of Marsupiata and Monotremata; in the last of which especially there is an approach to the oviparous type. We shall first consider the more common form of the mammiferous ovum. Of this the most marked characteristics are, as has already been stated, the very small size in proportion to the ovarian follicle, the finely granular yolk-substance, and the dense, clear, and firm external covering or zona pellucida.

The Graafian follicles, or ovarian vesicles, in which the ova are situated, attain, when mature, a size of from $\frac{1}{50}$ to $\frac{1}{4}$ or even $\frac{1}{2}$ an inch, varying in size in some measure with, but not in exact proportion to, the stature of the animals. In the human ovary these follicles are firm spheroidal sacs, which attain when mature an average size of about $\frac{1}{6}$ of an inch. In the ovaries of women, during the child-bearing period, a number of smaller follicles lie throughout the greater part of the substance of the ovary; the more developed follicles being usually placed towards the free surface, but at some little distance from it. As they enlarge and approach maturity, the ovarian substance appears to give way to them, or to become gradually thinner between the follicles and the outer surface of the ovary, so as at last to leave almost nothing but the covering membranes of the ovary at the most projecting part. Even when of their full size, however, the Graafian follicles of the human subject and of most animals do not project much beyond the general surface of the ovary;

Fig. 54*.



Mammiferous Ovum.

A. (*From Coste.*) Human ovary enlarged four diameters, partially dissected at *o o o*, to show the Graafian follicles in the ovarian stroma: one of these, more advanced, has had its double tunic *o v* cut into and reflected; the granular membrane *m g* has also been partially opened, showing the thickened portion or granular disc *d g*, in which the ovum is imbedded near the most projecting part. At *o v'*, another Graafian follicle has been burst, and the ovum in its granular disc is seen expelled from it.

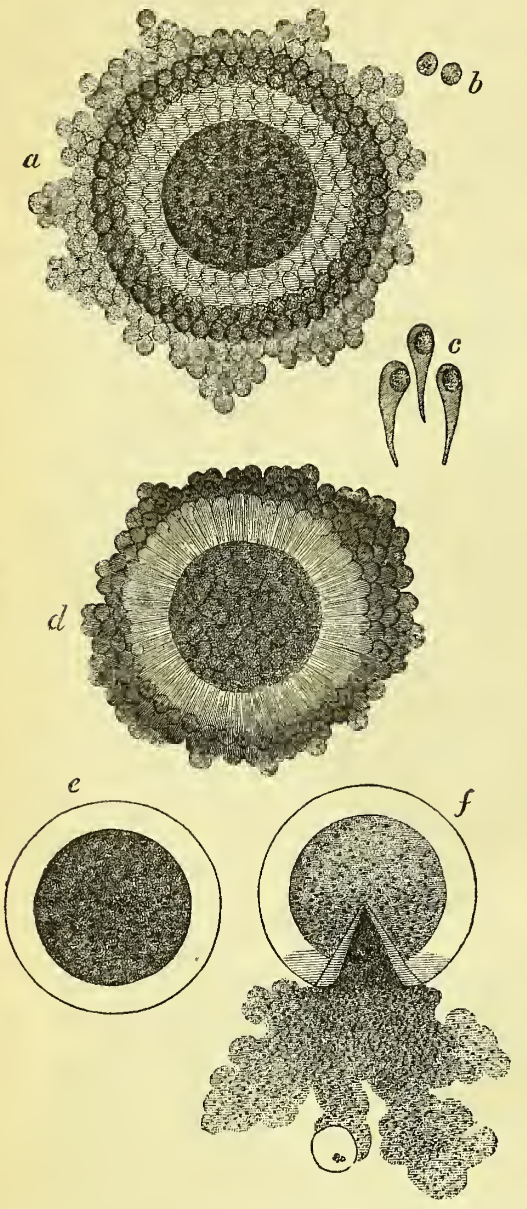
B. Transverse section of the human ovary, to show the general arrangement of the developed Graafian follicles towards the surface; twice the natural size.

C. Diagrammatic representation on an enlarged scale, in section, of two Graafian follicles, in different stages of advancement in the ovary of a mammifer. *p*, peritoneal covering of the ovary; *s t*, ovarian stroma; *o v*, the two layers of the ovisac; *m g*, membrana granulosa, near which is the discus granulosus, with the ovum imbedded.

but in some animals, in which the vesicles are proportionately more expanded, they extend beyond the general line of the surface in various places, and even sometimes give the ovary somewhat of the mammillated or grape-like appearance more common among oviparous animals.

The follicle is filled to distension with a clear albuminous fluid, which escapes with force when an incision is made through the membrane. Close to the inner surface of the follicle, and surrounding the fluid, is situated the layer of nucleated granular cells which has been termed *tunica* or *membrana granulosa*, from the opaque granular appearance of the cells composing it. These cells form a complete vesicular lining of the follicle; but throughout the greater part they cohere with only a moderate degree of firmness, so that the membrane readily tears when the follicle is opened. The minute ovum is imbedded in a thicker portion of this layer, the *cumulus* or *discus proligerus* of Von Baer, and is almost invariably situated close to the inner surface of the most projecting part of the Graafian follicle (see *fig.* 54*. A. and C., *mg.*) where in some animals, but not in the human ovary, the ovum may be detected in the undissected follicle through its coats and the ovarian coverings.

Fig. 55*.



Ovarian ovum of the Dog. (*From Bischoff.*)

a, magnified representation of the ovarian ovum of the dog, nearly mature, situated in the discus proligerus and part of the cells of the granular membrane; *b*, several detached granular cells.

d, another ovarian ovum of the same animal perfectly ripe, immediately previous to the rupture of the Graafian follicle; the cells of the proligerous disc have become of a pediculated shape; *c*, some of these cells detached.

e, the ovum from the same specimen as in *fig. a*, freed artificially from the granular cells of the disc, showing externally the thick clear zona or external membrane, and internally the opaque yolk substance: in the latter the germinal vesicle is obscured by the opacity of the substance surrounding it.

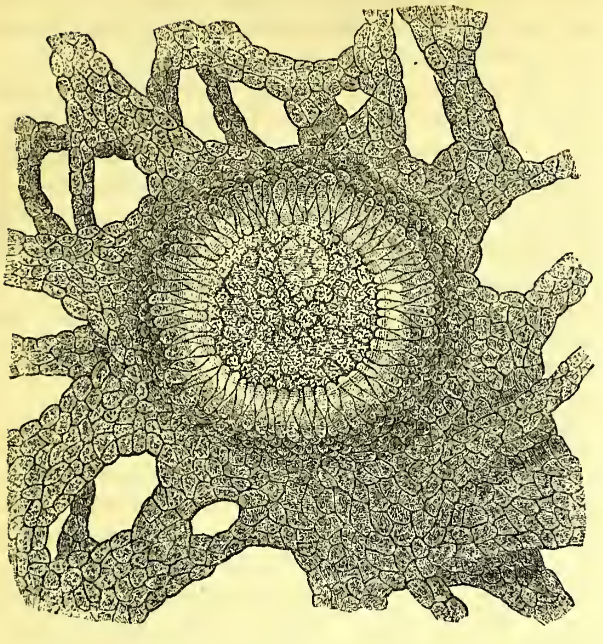
f, the same ovum burst by pressure, showing the contents of the ovum which have escaped, viz. the finely granular yolk substance and the germinal vesicle with its macula.

The cells of the membrana granulosa are in general about $\frac{1}{2400}''$ in diameter. They adhere with considerable firmness to the surface of the zona; so that when the follicle is opened and its contents are allowed to run upon a plate of glass for examination, the ovum is always found placed in its disc in a circumscribed attached portion of the membrana granulosa of about twice its own diameter. The ovum is itself of a nearly perfect spherical form when freed from pressure; but as it lies thus imbedded in the membrana granulosa, and moistened on a plate of glass, it gives rise to a slight rounded elevation in that membrane, which may easily be detected with the naked eye when the specimen is viewed sideways.

When the contents of the Graafian follicle are discharged naturally during life, a small aperture occurs nearly in the centre of the most projecting part of the wall of the follicle; and as the ovum lies near this place in the membrana granulosa, it is liable to be evacuated first, along with a portion of that membrane, which is soon torn away from the rest by the pressure of the fluid behind it, impelled by the contraction of the walls of the follicle and surrounding ovarian substance. During the descent of the ovum through the Fallopian tube the cells of the proligerous disc immediately surrounding the ovum alter their form, and are subsequently detached from the zona, so as to leave its external surface quite free and smooth. I have not, any more than Bischoff, been able to observe the four retaining straps or retinacula described by Martin Barry in his first series of Researches, as portions of the membrana granulosa naturally thicker than the rest, and which, radiating nearly at right angles from the proligerous disc, serve, as it were, to guide the ovum and its disc towards the aperture by which it escapes on the bursting of the follicle. The accompanying figure from Coste (56*.) gives that author's view of a structure somewhat similar to the retinacula of Barry.

The size of the mammiferous ovum itself is much more uniform among the different families of Mammalia than that of the Graafian follicle,

Fig. 56*.



Ovum of the Rabbit in the tunica granulosa.
(*From Coste.*)

The middle part of one of M. Coste's figures has been here copied to show the peculiar arrangement of the granular cells round the disc and ovum, which according to him are of the same nature with those described by Dr. Martin Barry as *retinacula*. It may be doubtful whether this structure is constant.

and bears no regular proportion in different families of animals to the stature of the whole body. In the mature state this variation extends from $\frac{1}{140}$ to $\frac{1}{260}$ or $\frac{1}{300}''$. The following are the results of a few measurements made by myself and others of the external diameter of the mature ovarian ovum, viz., man $\frac{1}{180}$, dog $\frac{1}{160}$, cat $\frac{1}{180}$, rabbit $\frac{1}{150}$, rat $\frac{1}{200}$, mouse $\frac{1}{220}$, pig $\frac{1}{200}$, cow $\frac{1}{250}$, guinea-pig $\frac{1}{240}''$.

The external tunic, or zona pellucida (a term founded on the description of Von Baer*, from its presenting the appearance of a transparent ring between the opaque granular yolk-mass within and the granular cells externally), is of great proportional thickness ; viz., from $\frac{1}{1500}$ to $\frac{1}{2500}''$, or from $\frac{1}{8}$ to $\frac{1}{12}$ of the whole diameter of the ovum. When entirely freed from the granular cells, its external surface appears smooth ; and the inner surface, which is exactly parallel to the outer, is also remarkably smooth. The substance of this tunic is very tough, and possesses considerable elasticity ; so that the ovum and its zona may be flattened by external pressure to a great extent ; and yet it regains its nearly spherical form when the pressure is removed. It is of glassy transparency and homogeneous ; neither any laminated, nor fibrous, nor other structure being perceptible under the highest magnifying power. It is easy to obtain evidence that it is one thick membrane, and not composed of two layers with intervening fluid, as some have held, by cleaving it with fine needle-points, when the cut edge becomes fully apparent. It has recently been stated by Remak*, that in the mature ovarian ovum of the rabbit, when freed from the granular cells, radiated lines may be perceived running quite through the zona pellucida ; these linear radiations, he conceives, indicate a peculiar structure of the zona, somewhat similar to the perforated condition of the outer membrane of the ovum in osseous fishes. I have perceived some of this radiated appearance ; but I am inclined to believe that it depends not on any structure of the zona itself, but rather on the marking produced by the adhesion of parts of the cells of the tunica granulosa, which become pediculated in very ripe ova, and have then a radiated appearance on the zona under pressure ; as represented by Bischoff in his view of the ovum of the dog, of which *fig.* 55 D. is a copy. I shall have occasion afterwards to state the nature of the fine canals which have been observed in the outer tunic of fishes' eggs.

It has been customary among ovologists, till very recently, to look upon the zona as corresponding to the external membrane of the yolk in the bird's egg. But from what has been already said in connection with that subject, the propriety of drawing a distinction between these two envelopes has been fully shown. I prefer, therefore, to retain the name of zona pellucida, though it may not be perhaps the best designation, as it prevents all confusion which might be introduced by views of its analogies. It will hereafter be more fully demonstrated that it not only differs in its mode of origin from the true vitelline membrane of birds, but that it also has a different destination in connection with embryonic development, inasmuch as, though formed in the ovary, it remains and constitutes the basis of, or becomes incorporated with, the important structure which at a later period becomes the chorion.

In the foregoing description of the membrane of the mammiferous ovum, I have adopted the view first advocated by Coste †, and by Thomas Wharton Jones ‡ ; and more fully brought out and established by the researches of Bischoff in his admirable works on the development of the Rabbit and the Dog. § It may be proper to remark farther, that though the name of zona pellucida has been employed to designate the thick single tough membrane by which, as is now well ascertained, the yolk of the mammiferous ovum is invariably enclosed from an early period of its formation in the ovary, this term is used synonymously with that of vitelline membrane, and as applied to

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[*] Epistola de Ovi Mammalium et Hominis genesi, Lipsiæ, 1827.

[*] Müller's Archiv. &c. for 1854, p. 252.

[†] Recherches sur la Génération des Mammifères, 4to. Paris, 1834, fig. 2. ; and Embryogénie Comparée, tom. i. p. 200, Paris, 1837.

[‡] In a paper read to the Royal Society of London in 1835 ; printed in the London Medical Gazette for 1838, p. 680.

[§] Entwickelungsgeschichte des Kanincheneies, Braunschweig, 4to. 1842 ; and Entwickelungsg. des Hundeies, Braunschweig, 4to. 1845.

the only covering with which the ovarian ovum is provided at the time of its leaving the Graafian vesicle, excepting that which it retains for a time derived from the cells of the tunica granulosa in the proligerous disc. Von Baer indeed, from whose description the term pellucid area or zone has been borrowed, was not fully aware of its consisting only of one thick membrane; and more than once, both in the Epistola and in the Commentary upon it, expresses himself doubtfully as to whether this pellucid space or halo* might not be formed of an external envelope which he terms the cortical membrane, and of another situated within it.

It is well known that when the mammiferous ovum has been fecundated, and arrives in the cavity of the uterus, and begins then rapidly to expand, it is covered by a membrane which soon undergoes great extension, and acquires a villous structure on its external surface, by which it may always be easily recognised. This villous envelope of the uterine ovum, universally now known as the chorion, is the product no doubt of changes which only occur in their completeness after fecundation, and as an accompaniment of embryonic development; but still as it appears probable that the zona pellucida is intimately connected with the first condition of the chorion, and as the first formation of the latter membrane is by many believed to take place independently of fecundation or fœtal development, it is necessary for me to make some remarks in this place on the relations of the zona pellucida to the external covering which the ovum obtains in the first periods of its residence within the female passages. This is a subject on which embryological writers are by no means agreed, and several of them indeed have themselves changed their opinions in regard to it in the progress of their researches.

Von Baer, the correctness of whose general views on the phenomena of development we have occasion to admire in almost every part of the subject of which he has treated, was at first of opinion that the chorion might arise in Mammalia from the outer of the two layers of which he at that time (though also doubtingly) conceived the external covering of the ovarian ovum to consist, and he looked upon this as a great difference or departure from analogy between the bird's egg and the ovum of the mammifer: but in his work on Development†, published eight years later than the Epistola and Commentary, he states his conviction from his observations, that in some mammiferous animals at least, such as the pig and sheep, the chorion is formed by external deposit on the surface of the ovarian ovum during its descent into the uterus, and therefore takes its origin more in analogy with the external covering of the bird's egg. At the same time he confesses that he was not able to reconcile this view with what he had seen in the dog and rabbit.

Valentin, in his Manual of the History of Development*, regarded it as most probable that the chorion is formed by the deposition and consolidation of an albuminous matter on the surface of the ovum during its descent through the first part of the Fallopian tubes; but though taking, as it appears, a perfectly correct view of this subject, he did not bring forward observations sufficient to establish the opinion which he had founded chiefly on analogical considerations.

We owe to Thomas Wharton Jones the first direct observation of the actual deposit of a layer of albuminous matter round the surface of the zona pellucida. But although Mr. Jones, in the observation which he made on the ovum of the rabbit within the Fallopian tubes on the third day after conception, was quite assured that a new structure had made its appearance in considerable thickness on the surface of the zona, yet he at first supposed that this might proceed from some change in the remains of the granular tunic which adhered to that membrane after it had left the Graafian follicle.† He afterwards, however, became aware of the source of this fallacy, and adopted the view that the mammiferous ovum receives a superadded structure, contributing to the formation of the chorion, in its descent through the tubes.

In the first series of his Embryological Researches, Martin Barry described not only the zona pellucida as recognised by other observers, but also a distinct vitelline membrane within it; and he conceived that the zona became afterwards the chorion. But in his second series he became aware, both from the statements of Wharton Jones and from his own observations, that a new deposit occurs in the rabbit's ovum; and this new deposit he now regarded as "the true chorion." He retained, however, for a time his view of the separate existence of a vitelline membrane; and thus described articulately three membranes as belonging to the mammiferous ovum, viz., vitelline membrane, zona pellucida, and chorion.‡ The first membrane he believed to disappear previous to the period of full maturity: the two last he regarded as together the source of the chorion of a later stage.

Bischoff also had not been aware from his earliest observations that any new deposit occurred round the ovum of the rabbit in the tubes; and even after he had become acquainted with this fact, and had observed it himself, as he did not detect a similar deposit on the ovum of the dog, he adhered to the view which he had previously taken, that the zona becomes the chorion, or at least that a new deposit is not in all Mammalia necessary for the formation of that membrane.

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* Spatium pellucidum, halo vel peripheria lucida. See Commentary on the Epistola, as translated by Breschet in his Repertoire, 1828, p. 52.

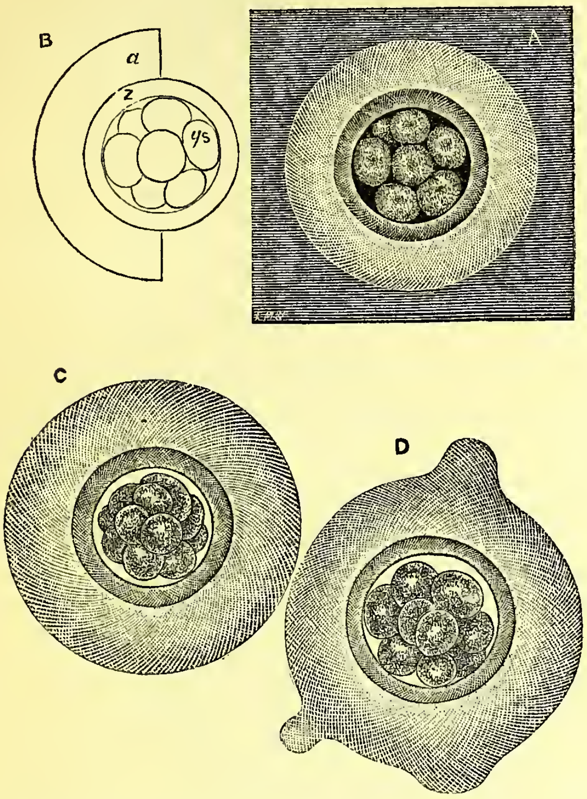
† Beobachtung. und Reflexion. über Entwickelungsgesch. &c., Königsberg, 1837, part ii. p. 185.

* Handbuch der Entwick. &c. des Menschen, Berlin, 1835, pp. 38, 39.

† On the First Changes in the Ova of the Mammifera, in consequence of Impregnation, and on the Mode of Origin of the Chorion, in Phil. Trans. 1837, part. ii. p. 339.

‡ See Phil. Trans. for 1839, p. 316.

Fig. 57*.



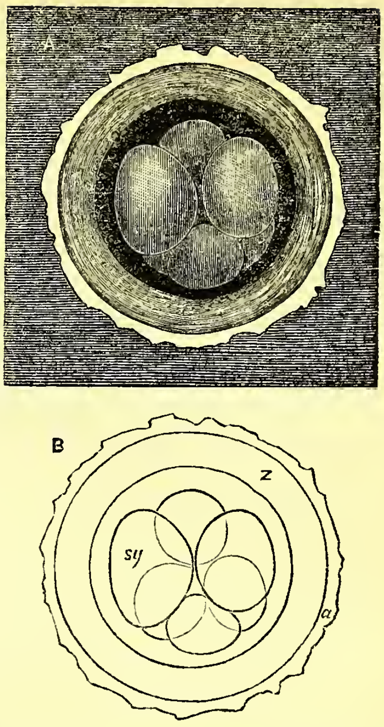
Ova of the Rabbit from the Fallopian tube three days after impregnation.

A, shows on a dark ground one of these ova, of which B is an explanatory outline. *y*, *s*, are the yolk segments of which there were eight; *z*, the zona; *a*, the thick layer of albumen which in this animal is always deposited on the exterior of the zona after the granular cells have been removed from it.

C and D. Other ova from the same animal; in D, are shown three projections of the albuminous covering which have been taken for villi of the chorion; but which according to Bischoff are not so. This ovum was farthest down in the Fallopian tube.

In a series of observations made by myself on the ovum of the dog and rabbit during their descent from the ovary to the uterus, in the summer of 1840, I was induced to adopt the opinion that a new deposit does really occur on the surface of the ovum in both of these animals. I repeatedly observed the large gelatinous or firm thick albuminous covering on the rabbit's ovum when it had just entered the cavity of the uterus; and in several instances I thought I could perceive the first formation of the villi of the chorion by sprouting or budding from the surface of the newly deposited substance, which, as in Wharton Jones' and Barry's observations, it was quite easy to distinguish from the membrane of the zona. In the ovum of the dog I admit, with Bischoff, the appearance is very different; but yet my observations appeared to me to demonstrate that in that animal also a substance is superadded to the surface of the zona, for that membrane, which presents at an earlier period a perfectly distinct and smooth outline on its external surface, becomes in the course of the descent through the Fallopian tubes and by the time of its first arrival in the uterus, not only irregularly flocculent on its surface, but also thickened; in fact, presents all the appearance of a granulo-mucous substance having been deposited upon it.

Fig. 58*.



Ovum of the Dog from the Fallopian tube ten days after impregnation.

A. The yolk has undergone division into eight segments, and there is a thin irregular deposit of albumen on the outer surface of the zona. (This is represented too light in the figure.)

B. Explanatory outline of the same; *y*, *s*, yolk segments; *z*, zona pellucida; *a*, layer of albumen, from which in connection with the zona the chorion takes its origin.

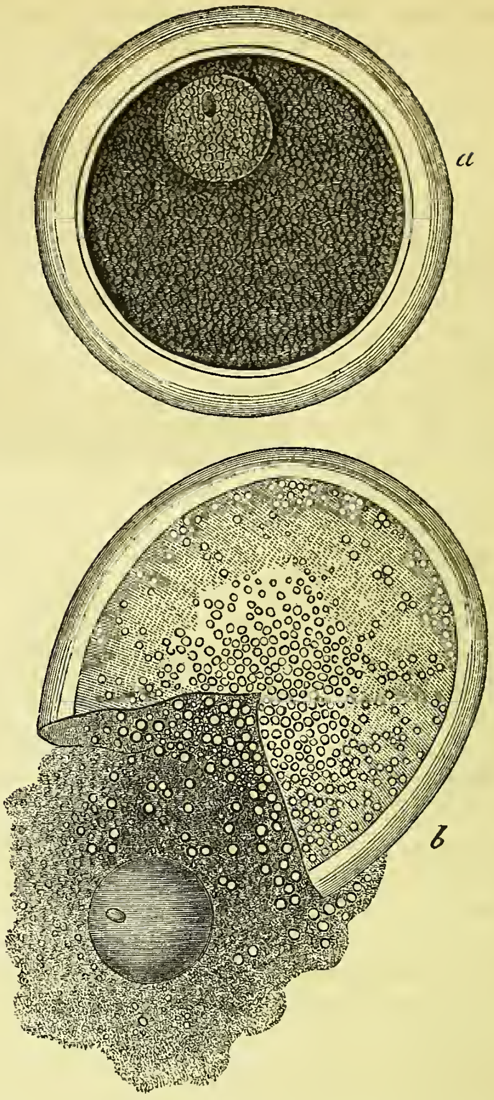
It may be proper to explain here, that it has now been fully shown by Bischoff's excellent observations, that in both the animals mentioned, and also in the guinea-pig, the cells of the tunica granulosa, which adhere to the surface of the zona when it leaves the Graafian follicle, are completely separated from it within the first two or three days of the residence of the ovum within the tube, so as to leave the external surface of the zona perfectly smooth. Bischoff has shown, indeed, as I have also repeatedly observed, that a change has occurred in the cells of the proligerous disc, adherent to the ovum while it is still within the ovary, which indicates its approaching maturity. This change consists, as already stated, in these cells becoming somewhat spindle-shaped or pyriform, their narrow or pointed ends being attached to and radiating from the surface of the zona. (See as before *fig.* 55. D.) It is quite easy, therefore, after this separation takes place, to distinguish any change by addition of new matter or otherwise which the surface of the zona may undergo. No one can fail to perceive the addition to the ovum of the rabbit, the diameter of which is thus increased between two and three times, so as to give it somewhat the aspect of the ovum of a Batrachian in miniature; and in the dog it has appeared to me that the increased thickness and more opaque and flocculent roughness of the surface of the zona were sufficient proofs of a new deposit having taken place. This deposit, no doubt, becomes very completely incorporated with the substance of the zona, and is not easily to be distinguished from it; but in one or two instances I have thought that I was able to perceive a line of demarcation between them. Several of Bischoff's very faithful figures seem to me even to represent this deposit as it has occurred on the ova of the dog. But his statements in his work on the Development of the Guinea-Pig * are so precise against the occurrence of such a deposit, that further observations will be required fully to determine the question whether it is of constant occurrence or essential to the formation of the chorion.

Later observations lead me to think that I may have been in error in supposing that the villi of the chorion grow directly from the albuminous deposit. These villi, which, as I have said, form a most characteristic feature of the external covering of the mammiferous ovum in the course of development, begin to be formed only when the ovum has reached the cavity of the uterus. The time of the formation of these villi, as well as their size, varies, however, considerably in different animals, and probably also to some extent in the same animal.† They are developed from the external surface, and their structure is at first nearly homogeneous, or at least only slightly granular; they afterwards acquire a cellular structure, and in the course of fœtal development become at an early period the seat of a complicated vascular growth, by which the relations of the maternal parent and offspring are maintained through utero-gestation. But the fuller description of this part of the growth of the chorion belongs rather to the history of development after fecundation. My present object has been only to show the relation of this membrane to the zona or ovarian coverings of the ovum.

The contents of the ovum or parts within the zona consist of the yolk-mass or yolk-substance, and the germinal vesicle. The first of these constitutes a spherical mass of variable consistence, in which granules, or molecules and globules of various sizes, from the most minute up to about $\frac{1}{6000}$ or $\frac{1}{4000}''$, are suspended in a fluid. The proportion of the granules to the fluid varies to a considerable extent in different animals, the ovum being much more opaque, and usually of a dull-yellow colour when the granules are in large quantity, as is the case in most Carnivora, and may be easily seen in the dog or cat. The clear fluid in which the granules are suspended varies also in its consistence, being of a marked viscid quality in some instances, and thin and limpid in others; so that in some animals, when the zona is punctured, the yolk-substance flows freely out, while in others, and this is the case in the human ovum, the yolk-substance holds together as one consistent mass. The yolk-substance does not adhere in the slightest to the interior of the the zona, but on the contrary is readily detached from it; and in some instances, in the entire unimpregnated ovum, a space is seen between the yolk-substance and the zona, formed apparently by the imbibition of water between them. This separation between the yolk-substance and zona appears to be, at a later period, a constant and probably important change in connection with fecundation and development.

The granules of the yolk-substance are generally rather more densely set together and

Fig. 59*.



Ovarian ovum of the Rabbit. (*From Coste.*)

a, ovarian ovum extracted from a nearly ripe Graafian follicle, and freed from the adherent granular cells; the close set granules of the yolk substance, among which the germinal vesicle is perceived with a slightly oval macula or nucleus, are well represented.

b, the same burst by pressure; the yolk granules adhering together by a viscid clearer fluid substance are seen escaping from the large aperture in the zona along with the germinal vesicle.

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* Entwickelungsg. des Meerschweinchens, 4to. Giessen, 1852.

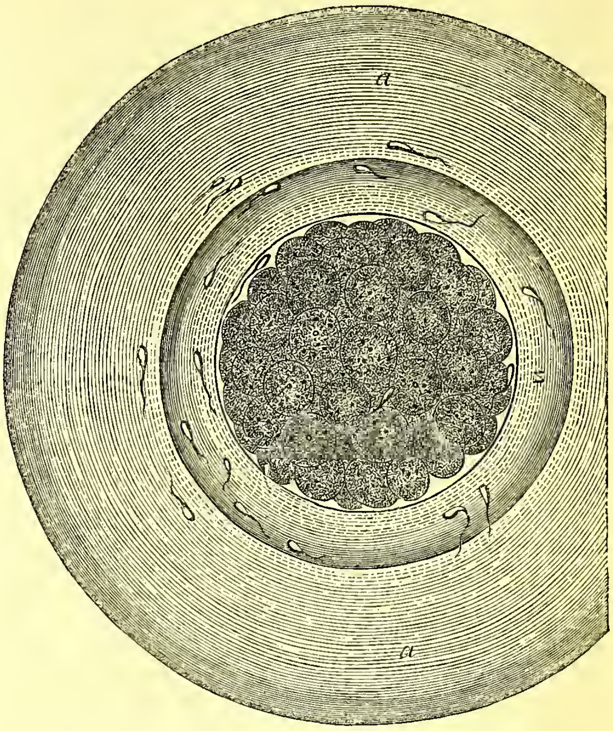
† Barry and Bischoff.

more firmly united towards the external surface. This circumstance has given rise to the belief among some observers in the existence of an additional delicate membrane enclosing the yolk-mass; but the most attentive observation by Bischoff, Wharton Jones, myself, and others has failed to detect such a membrane; and there is reason to think that the confident belief in its existence has had its origin in part at least in a desire to establish a more complete analogy between the ovum of birds and Mammalia, and to find accordingly a vitelline membrane as well as a chorion present in the ova of the latter.

The germinal vesicle is usually about a sixth of the diameter of the whole ovum; but it is sometimes larger, or between a fifth and a fourth. It possesses a delicate membranous wall of a spherical or spheroidal form and homogeneous structure: it is barely possible to observe the double line of the thickness of this wall with the quarter of an inch lens in the microscope. In most animals the germinal vesicle is readily distinguishable from the rest of the ovum by its superior clearness, excepting in those instances in which it is hidden by the great opacity of the yolk-substance; but then it may generally be made manifest by flattening the ovum by compression between plates of glass. The fluid which fills its cavity, which is generally very clear, contains some minute granules in suspension; and besides these there is apparent within it the macula germinativa or germinal nucleus. This last, which is in general well defined in the mammiferous ovum, varies slightly in different animals: in some presenting the appearance of a round globule, with a delicate circumscribing line almost amounting to a vesicular covering; but more frequently it consists only of a small spherical or discoid mass of fine granules. In a germinal vesicle of $\frac{1}{600}''$ in diameter, such as that of the rabbit, the diameter of the macula is about one-fourth of that of the vesicle, or $\frac{1}{2400}''$.

In the earlier stages of formation of the ovum the germinal vesicle is of smaller size; but it is then proportionally larger than the other parts. It is the part of the ovum first formed; the yolk-substance, which is subsequently deposited in gradually increasing quantity round it, together with the zona, grow at a more rapid rate than the vesicle, and thus the latter remains in the mature state proportionally smaller. As the yolk-substance is at first deposited nearly in equal quantity on every side of the vesicle, it for a time contains the vesicle in its centre; but as the formation of the ovum proceeds the vesicle is found in general to have approached the surface at one side of the yolk-substance; and in the mature ovum the vesicle seems to be imbedded in the most compact and superficial layer of fine granules of the yolk-substance. This place no doubt corresponds in Mammalia, as has been ascertained in Batrachia, to the point from which after fecundation the first cleavage of the yolk proceeds; but this fact has not yet been determined by observation in the Mammalia, nor has any one as yet succeeded in observing a canal or pore leading from the surface of the yolk-substance towards the germinal vesicle in the mammiferous ovum.

Fig. 60*.



Ovum of the Rabbit from the Fallopian-tube with spermatozoa.

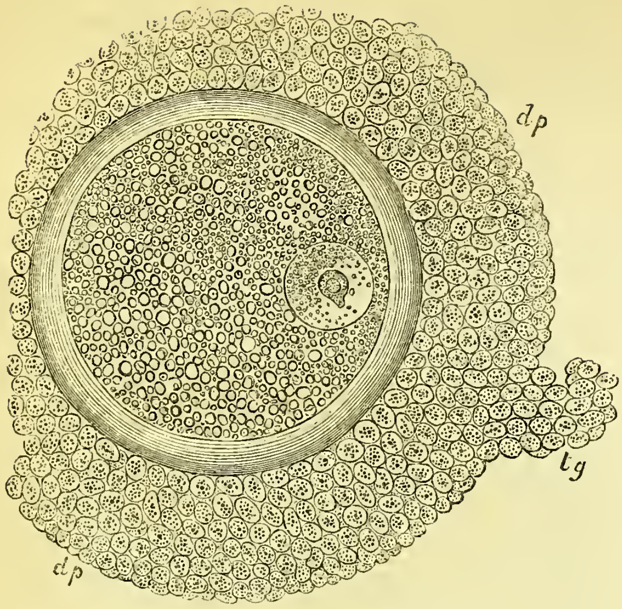
The accompanying figure is introduced to show the usual position of the spermatozoa in relation to the zona and albuminous layer in the ovum of Mammalia during and after impregnation. This ovum is magnified 250 diameters. It was taken along with five others from the lower part of the Fallopian tube 68 or 70 hours after impregnation. The segmentation appears to have proceeded to the fifth stage. There is a thick covering of albumen over the zona, and a number of spermatozoa are represented involved in the albuminous substance; some were also seen on the surface of the zona, and some, varying in number in the different ova observed from five to seven or nine, were clearly ascertained to be situated within the zona on the surface of and in the grooves between the yolk segments. The position of these last is not sufficiently clearly represented in the figure.

In the situation now described the germinal vesicle, though not by any means firmly fixed, is yet sufficiently embraced by the yolk-substance to prevent it from changing place when the ovum is moved in different directions. In the instances of the more fluid condition of the yolk it flows freely out from within the zona when this has been broken; but in those ova in which the yolk-substance is more viscid, as in the human ovum, we generally fail to isolate the vesicle from the rest of the substance.

The macula or nucleus appears to be attached to the inner surface of the membrane of the germinal vesicle. This is especially seen to be the case in the Pig, in which the macula seems to be somewhat pyriform or pediculated (see *fig.* 61*).

No important changes have been observed

Fig. 61 *.



Ovarian ovum of the Sow.

This ovum is represented in order to show the peculiar pyriform shape of the macula in the germinal vesicle, to the wall of which the macula appears to be attached. This ovum was taken from a Graafian follicle of $\frac{1}{12}''$ in diameter. The following are the dimensions of its several parts which are magnified 250 diameters in the figure. The ovum across the exterior of the zona $\frac{1}{175}''$; the vitellus $\frac{1}{200}''$; the germinal vesicle $\frac{1}{750}''$; the macula $\frac{1}{2100}''$; thickness of the zona $\frac{1}{2100}''$. The ovum is surrounded by the thick layer of cells which form the granular disc, *dp*. A few cells of the thinner membrana granulosa are represented at *tg*.

to occur in the germinal vesicle during the ovarian existence of the ovum. It usually disappears in Mammalia previous to the escape of the ovum from the Graafian follicle; but in this class of animals the phenomena attending the disappearance have not yet been fully investigated. There are some grounds for believing that immediately previous to the bursting of the vesicle there may be changes of the macula and other contents of the vesicle of a corresponding nature with those which have been more clearly observed in Batrachia and Fishes. Dr. Martin Barry seems to have observed something of this kind, and M. Coste has figured, but not so far as I am aware described, the development of cells in the germinal vesicle of a ripe ovarian human ovum.*

R. Wagner states, that occasionally a double macula may be seen in the germinal vesicle.† I have on one occasion observed two germinal vesicles within the same ovum in the dog.

Bischoff has on three occasions observed two ovules in the same Graafian follicle of the rabbit.‡ This had been previously noticed by Von Baer in the dog and pig. And Bidder § detected two ovules embedded in the same granular membrane of one Graafian vesicle of the cow. Upon the question how far these varieties in the structure of the ovum may be supposed to be related to the origin of Double-monsters and Twins, I must refer to Professor Vrolik's interesting article Teratology.*

For the assistance of those who may wish to engage in researches of the same nature as those by which the above facts have been ascertained, I will state shortly the manner in which the ova of Mammalia may be procured either from the ovary or after they have left that organ. 1st. For the examination of the earlier ovarian ova and follicles, thin sections of the ovarian substance are to be made, especially towards the surface of the ovary; and some of these are to be teased out with needle points, and examined with the aid of compression, &c. 2nd. For the more mature ovarian ovum, &c., the outer covering of the ovary is to be removed from the surface of one or more of the prominent follicles; and the latter may then, if large, be carefully dissected out of the ovary, and laid on a glass plate, where it is to be opened with a sharp-pointed knife, and its contents are to be gently pressed out on the glass. The ovum may in general be easily detected in a part of the tunica granulosa with a low magnifying lens, or even sometimes with the naked eye. In the ovary of the dog the ovum may sometimes be seen without any dissection towards the most prominent part of the surface of the mature follicles.† 3rd. To procure the ova after they have left the ovary, or while they are in the tubes, two methods may be pursued: either the whole length of the tube may be opened with very finely-pointed and sharp scissors, and the surface then spread out and examined carefully with a low magnifying power under a good elumination, but this must not be done under water; or another plan may be followed according to the recommendation of Martin Barry, founded on a suggestion thrown out by Cruickshank, as follows: The Fallopian tubes being divided into several portions, the contents of each portion are to be separately pressed out by passing a blunt instrument firmly along the outside of the tube, and, being placed on suitable plates of glass, are to be subjected to the necessary examination. The latter method is particularly convenient in small animals: in the larger I have followed both plans. The method of Barry certainly saves much time and trouble, and is on the whole sure enough.‡ 4th. Of the plan for obtaining the ova from the uterus, when of considerable size, as it belongs rather to the history of development, I will only say here that the greatest caution is necessary in cutting through the walls of the uterus in different layers so as to avoid injuring the ova, and that the examination must be made at first in the dry state.

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* See the plate in his great work marked "Mammifères; Homme." Pl. I. Fig. 6.

† See Prodromus Hist. Generationis, Fig. xxxi.

‡ Müller's Archiv. Jahrsbericht, p. 169.

§ Müller's Archiv. 1842, p. 86.

* Vol. iv. p. 973. Cyclopæd. of Anat. and Physiol.

† See Von Baer's Commentary on his Epistola, in Breschet's Répertoire, 1828, p. 38.

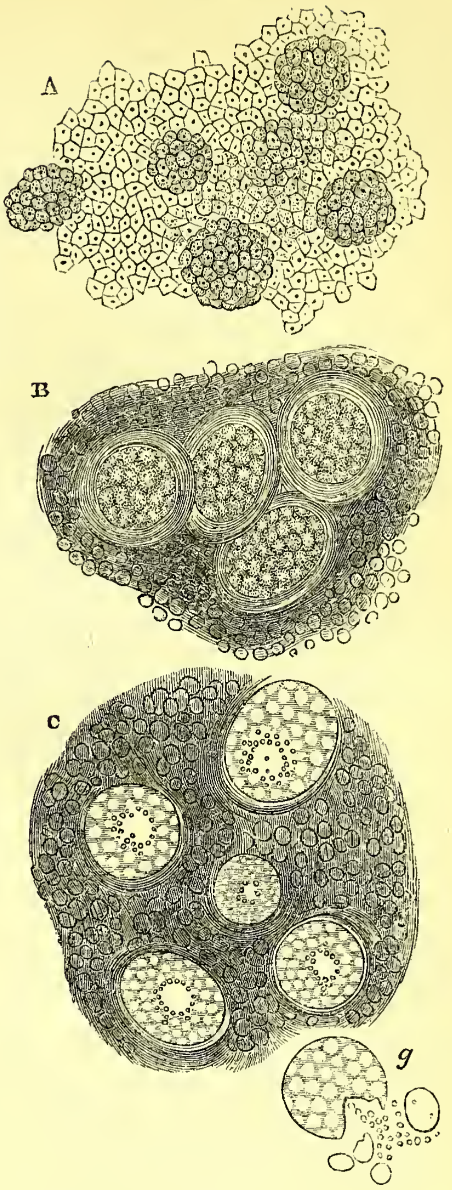
‡ See Barry's Second Series of Researches, &c., Phil. Trans. 1839, p. 366.

Origin and Formation of the Mammiferous Ovum.—This subject has already been adverted to in the previous section in connection with the history of the formation of the bird's egg. Dr. Martin Barry was led, by his numerous observations, to form the conclusion, that the germinal vesicle is the first part which makes its appearance in the ovarian stroma at the commencement of the formation of the ova. All observers seem now to be agreed, that of the parts belonging strictly to the ovum itself, the germinal vesicle is the first formed; but the observations of Valentin, Bischoff and others appear rather to support the view, which is opposed to that of Barry, that the Graafian follicles may be detected in the ovarian stroma before any part of the ovule is distinguishable.

The ovules are formed at a comparatively early period in the ovary. Carus was the first to point out * that in the ovary of the human female child the follicles containing distinct ovules are perceptible at birth. Vallisnieri had long previously, it appears, made a similar observation. Bischoff has, with more precision, pointed out, that there is considerable variation in different children of the same age as to the degree of advancement of the germs of ova within the ovarium; in some nothing more than a perfectly uniform ovarian stroma is perceptible at birth, while in others the follicles are distinctly formed, even at an earlier period. By the age of ten or eleven years a number of the vesicles are found to be approaching maturity, and almost all have left their earliest condition. Both Barry and Bischoff, however, are of opinion that new sets of Graafian follicles and ova may continue to arise within the ovaries during the whole child-bearing period of the human female; and there can be little doubt that this takes place in most of the lower animals.

Bischoff describes the Graafian follicles as taking their origin from minute heaps of granules in the ovarian stroma; but he has not been able to confirm the statement of Valentin that the earliest follicles proceed from primitive gland tubes stretching from the attached border towards the surface of the ovary.† In various animals the follicles and ova begin to be formed at an earlier period than in the human female: according to Bischoff, they arise very early both in the cow and pig.

Fig. 62*.



Development of the Ovarian ovum of Mammalia. (*From Bischoff.*)

A represents a very small portion of the ovary of a fœtal dog. The commencing Graafian follicles are visible in the granular or cellular stroma of the ovary, constituting dark heaps of more opaque granules or small cells.

B, fragment of the ovary of a dog three weeks after birth. The Graafian follicles are now seen in the fibro-granular ovarian stroma, each surrounded by a homogeneous and fibrous covering, and filled with granules.

C, fragment of the ovary of a pig three weeks old. The Graafian follicles are now seen to be formed of a fine transparent vesicular membrane, and round the larger ones fibres are beginning to be deposited. The wall of the follicles are lined internally with delicate epithelial cells. The germinal vesicles now visible within consist of a fine clear cell with a nucleus or dot, and a few vitelline granules have begun to be deposited round the germinal vesicles.

g, one of these Graafian follicles burst with a needle, showing the contents of the follicle; there being as yet no zona or vitelline membrane.

When the primary follicle can be perceived, it consists of a small vesicle scarcely more than $\frac{1}{1000}''$ in diameter. To this primary vesicle Martin Barry has given the appropriate name of Ovisac. Soon afterwards, when the vesicle has expanded somewhat, it is found to contain the rudiment of the ovum; first in the shape of the very small germinal vesicle, generally surrounded by a small quantity of granular fluid. Soon afterwards the outer follicle is lined with a few extremely delicate or hyaline hemispherical cells, which have somewhat the appearance of those of epithelium, and which thus give rise to a clear space between the membrane or wall of the follicle, and all that yet exists of the ovule. Next, the yolk substance is formed round the germinal vesicle; first of all, as has been shown by Leuckart[†], by the deposit of a clear viscid fluid, and next by the formation of dark or opaque small granules in this fluid adjacent to the germinal vesicle. Somewhat later the zona pellucida, which cannot be said to have existed from the first, comes to be apparent outside the opaque granular substance of the yolk, and close to the epithelial cells which line the follicle: it seems as if it owed its origin to the condensation of the outermost layer of the clear basement matter from which the yolk-substance is formed.

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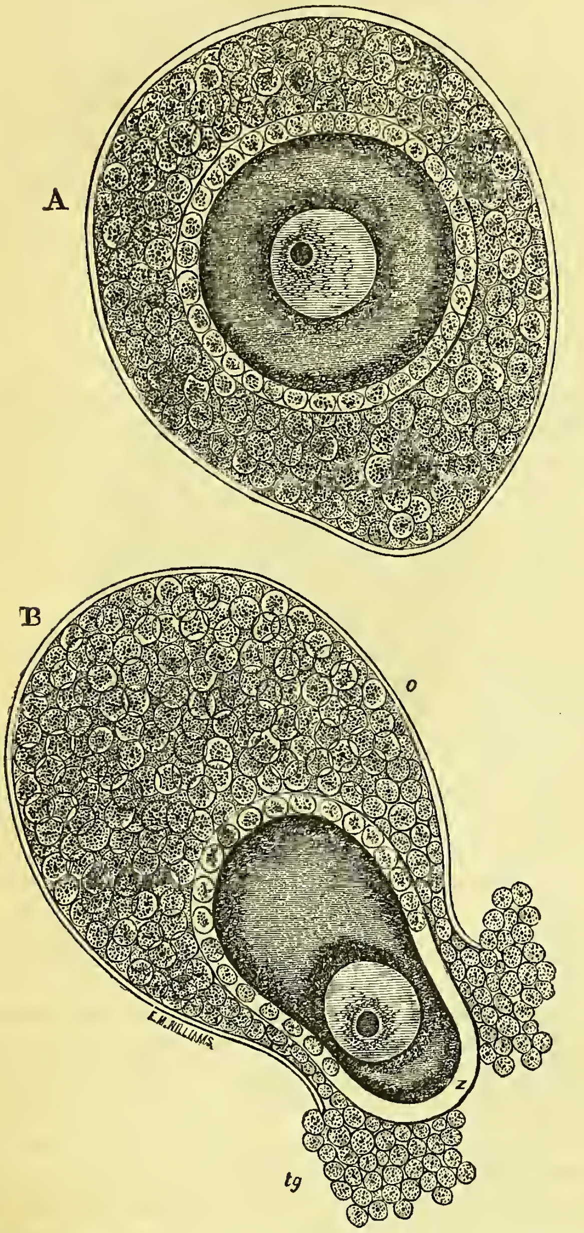
* Müller's Archiv. for 1832, p. 379.

† Handbuch der Entwickelungsgeschichte, 1835, p. 389.; and Müller's Archiv for 1838, p. 529.

Fig. 63 *.



Ovarian follicle and ovum of the Rabbit at an early stage.

The follicle here represented was about $\frac{1}{100}$'' in diameter: in the figure it is shown as it appears under slight pressure. All the parts of the ovum are distinct, and its large size in proportion to the follicle and tunica granulosa is apparent. In the lower of the two figures the follicle is represented as having been burst by pressure and the ovum with the tunica granulosa in the act of escaping from within: the yielding character and elasticity of the zona is shown by the change of form during the escape, and the ovum afterwards regaining its spherical shape. *o*, the wall of the follicle; *t g*, the tunica granulosa; *z*, the zona partially freed from the cell covering. The macula with the germinal vesicle is remarkably distinct, and is surrounded by a quantity of fine molecular substance.

The membrana granulosa consists for a time of a single layer of nucleated epithelial cells situated between the ovule and the Graafian follicle. The latter not being yet expanded by fluid, is at this period completely filled by the ovum. Such is the state of the parts, now all present, in follicles of from $\frac{1}{100}$ to $\frac{1}{200}''$ in diameter. Subsequently the follicle increases in size much more rapidly than the ovum; the membrana granulosa follows closely the wall of the follicle in its rapid expansion by the increasing accumulation of fluid within; and the ovum is now found to be imbedded in a particular portion of the layer of granular cells constituting the *cumulus*.

According to the best observations, then, as to the formation of the mammiferous ovum, it appears that the ovarian follicle, which we may look upon as the primary gland cell, is first produced; that within it at a very early period the germinal vesicle with its nucleus next arises, and that very soon after the origin of this primary part the yolk-substance commences by a deposit of fluid and granules round the germinal vesicle; that the Graafian follicle is lined by a layer of nucleated cells resembling epithelium, which constitute the commencement of the tunica granulosa; that the zona pellucida, which forms the outermost covering of the ovum when it leaves the ovary, is formed at an early period, but somewhat later than the commencement of the other parts of the ovum; and that it probably owes its origin to a membranous condensation of the outermost part of the clear primitive yolk-substance; and that, finally, the tunica granulosa increases in quantity and extent, is expanded along with the follicle by the fluid within it, and being deposited at its thickened cumulus round the ovum encloses it in a part of its substance.

The structure of the ovum is, on the whole, very similar throughout all the families of the class Mammalia in which it has been examined, excepting one, viz., the Monotremata. In Marsupialia, in which, from the remarkable deviation from the more common mode of gestation, it has been supposed that the ovum might present some peculiarities, it does not appear, from the observations of Professor Owen, that any remarkable difference is to be detected. In the ovisac there was observed a somewhat larger quantity of granular substance than usual; but the diameter of one of the largest ova in the *Macropus Parryi* or Kangaroo was not greater than $\frac{1}{120}''$, and the germinal vesicle was only $\frac{1}{1680}''$, which is proportionally small; so that it cannot be held that in this animal there was apparent any approach to the oviparous type.

In the Monotremata, however, the ovum is of much larger size, and appears to occupy the whole or the greater part of the ovarian follicle or capsule; more in the manner of that in birds and scaly reptiles. According to Professor Owen*, the ovaries of the Ornithorhynchus present numerous elevations on their surface caused by the projection of ovisacs of different sizes and in different stages of development. The largest of these sacs have a diameter of two lines; and, as in birds, though in a less marked manner, the right oviduct and ovary are less developed than the left. The unimpregnated ovum nearly completely fills the ovisac or ovarian capsule. The germinal vesicle is of a comparatively large size, being about $\frac{1}{250}''$ in diameter. The vitelline substance is rich in nucleated (?) cells or granules, intermixed with clear colourless oil globules. The vitelline membrane is moderately thick and smooth, and refracts light strongly. The ovum is separated from the inner surface of the ovarian capsule by a very small quantity of fluid, and by a stratum of granules or cells.

[†] Article Zeugung in Wagner's Handworterbuch der Physiologie, 1853.

The ova found in the uterus of the Ornithorhynchus were of a deep-yellow colour, with a smooth polished surface, and had no adhesion to the inner uterine membrane. In one animal the yolks were found enclosed in a more transparent mass, which was surrounded by a cortical membrane of some tenacity, presenting in fact some resemblance to the albumen and shell membrane of a bird's egg. Leuckart † thinks it probable that Owen may have been misled as to the size of the ova by the examination of specimens which had been preserved in alcohol; but Professor Owen informs me, that he was fully on his guard against such an error, and was quite satisfied of the approach in the structure of these ova to the oviparous type of birds and reptiles.

I have examined the ovaries in a specimen of *Echidna hystrix*, which has been preserved in alcohol; and although the somewhat deteriorated state of the specimen, and the circumstance of the ovaries not being in the fully developed condition, were not the most favourable for minute observation, I was convinced that the ovarian ova of this animal, like those of its congener the Ornithorhynchus, belong rather to the oviparous than to the usual mammiferous type. The yolks, which quite filled the ovisacs, were some of them about $\frac{1}{20}''$ in diameter: they contained a large quantity of granular globules similar to the yolk corpuscles of birds; the yolk, in fact, consisted of the nutritive as well as the formative substance; and the whole aspect of the ovary, as well as of the individual yolks, recalled to my mind that of an oviparous animal in a somewhat undeveloped state.

The ova of a considerable number of the Invertebrate animals belong to the same group under which I have placed that of Mammalia; that is, they consist principally of formative or granular yolk-substance, undergo complete segmentation, and have a simple zona or structureless covering; but yet the varieties in structure, relations, and mode of production among these ova themselves, and their differences from the ova of Mammalia are so great, that I think it will conduce to greater clearness and prevent repetition, to defer treating of the ova of Invertebrata till after I shall have given the description of the remaining ova of the Vertebrate animals, to which we shall now proceed.

Third Group of the Ova of Vertebrate Animals.—Under this head I have now to state some details as to the structure, relations, and mode of formation of the ova of amphibious reptiles or chiefly the Batrachia, and of osseous fishes. The ova of both of these tribes of animals appear to occupy an intermediate place between the very small and granular-yolked ova of the Mammalia and the large cellular-yolked ova of birds and scaly reptiles. They agree in both possessing a yolk of moderate size, in the substance of the yolk being principally or largely of the formative kind, and in the possession of a proportionally large germinal vesicle, in which the macula is not a single nucleus, but rather a large collection of nuclei or maculæ. In both of them the segmentation is partial or not complete, affecting chiefly the superficial part of the yolk, in which the formative or germinal portion of the yolk is placed, but varying considerably in the depth and the extent of the surface which it involves in different species and genera, more especially among the Amphibia. In the predominance of the formative yolk and in its relations to the process of segmentation, therefore, they approach the Mammalia, while in the large size and structure of the germinal vesicle in all, and in the considerable amount of nutritive yolk in some, they more nearly resemble the group of large-yolked ova. It will be proper, on account of the differences between them, to describe separately the ova of Amphibia and those of Osseous fishes.

Amphibia.—Batrachia.—The ripe ovarian ovum of the common frog or toad is a nearly spherical body of from $\frac{1}{15}$ to $\frac{1}{12}$ of an inch in diameter, of a dark colour, contained within and closely embraced by a thin vascular sac formed by the dilatation of the ovisacs which hang into the general ovarian cavity.

This capsule or ovisac is attached to the rest of the ovarian substance by a broad band rather than by a narrow pedicle; and when the yolk or ovarian ovum is mature, it escapes from the ovisac by the formation of an aperture in the remote or free side of this capsule, somewhat in the same manner as occurs in the calyces of the bird, but with a wider aperture. Through the apertures of the general ovarian capsule the numerous ova pass into the abdominal cavity, during the first period of sexual union, and they are thence taken up singly by the open upper extremities of the two oviducts ; through the whole of which canals they descend, and in their passage receive an additional covering of a peculiar gelatinous or albuminous substance, which adheres closely to the surface of the yolk membrane, and is firm and of comparatively little bulk while the ova are still within the oviduct, but which after exclusion rapidly swells by the imbibition of a large quantity of water, so as to become several times its original thickness, and to assume a soft gelatinous consistence.

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* See Prof. Owen's Article Monotremata in this Cyclopædia, and his Memoirs in the Philos. Trans. for 1832 and 1835. See in particular figures 191, 192, and 194 of the article Monotremata, Cylopæd. of Anat. vol. iii. p. 393, et seq.

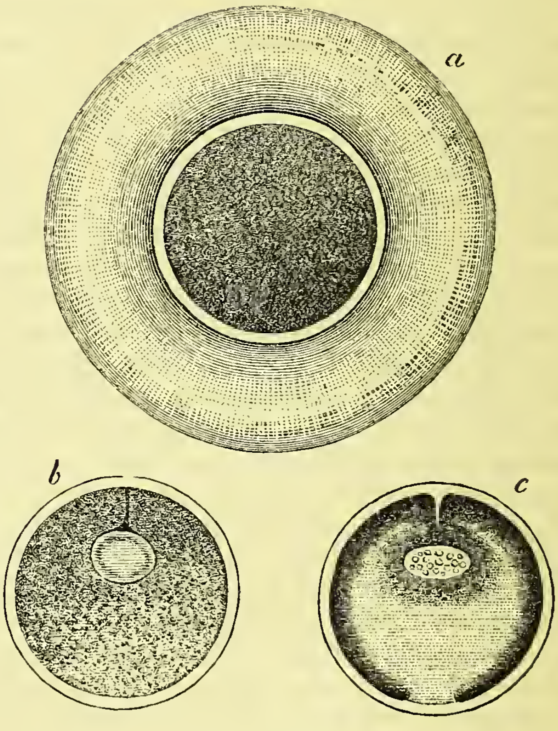
† Article Zeugung, p. 783.

The ova which have passed through the oviducts remain for a time accumulated in large numbers in a dilated part of the canals near their lower end, until the whole or greater part of those which are ready to descend from the ovary have passed down ; and then, while the male still continues united with the female, the ova are rapidly excluded, and the male sheds the spermatic fluid in abundance, partly on the ova as they pass into the water, and partly after separating from the female, upon the spawn as it floats in the water. The importance of the imbibition of water by the gelatinous covering immediately on the exclusion of the ova and just at the time when the spermatic fluid has been placed upon them, in securing the access of the spermatozoa to the surface of the vitelline membrane through the stiff jelly, and in thus promoting fecundation, will be afterwards more particularly adverted to.

In the tailed Amphibia, such as the different kinds of Newt (Salamandra, Triton, and Lissotriton) there is not the same union of the male and female as in the tailless or Anurous Batrachia ; and impregnation takes place by the entrance of the spermatic fluid, shed in the water by the male while placed near the female, into the oviducts of the latter. In these animals the external covering consists of an elliptical membranous capsule filled with a clear fluid and containing the coloured spherical yolk ; but there is also externally a small quantity of gelatinous substance which in some of them serves to attach the ova to leaves of plants or other objects. In the common larger and smaller newts the ova are in smaller number than in the frog or toad, and are excluded one by one by the female, which deposits them singly in a folded leaf or other place of security.*

The yolk of the ripe ovarian ovum in Amphibia consists of a thick opaque mass of vitelline substance, within which and towards one side the large germinal vesicle is placed. The vitelline substance is usually of a darker colour on the exterior and lighter in the centre. In the common toad the superficial part is almost black ; in the common frog, *Rana temporaria*, it is of a very dark brown ; and it is in different other species of various hues, as stated in a former part of this article. The dark superficial part does not in general cover the whole surface of the yolk, but is deficient on one side ; and its extent as compared with the inner paler part, which appears where the dark part terminates, varies in different species and is greater in proportion to the degree of advancement of the ova. In some species, as in the *Alytes obstetricans*, of which C. Vogt has given an excellent description†, it does not, when the ovum is mature, occupy more than a half of the surface ; but in the common frog and toad it covers so much of the surface of the yolk when it is about to leave the ovary, that the gray internal part is only seen as a defined round spot on the opposite side. In the undeveloped ovarian ova, however, the dark part is much more limited in its extent, thus allowing a greater part of the lighter-coloured internal part to be seen.

Fig. 64 *.



Ovum of the Frog.

a. (*From Newport.*) An ovum of the frog half an hour after impregnation, covered with its gelatinous mass. The dark part of the egg or yolk is seen to be surrounded by a vitelline membrane. Spermatozoa were seen everywhere in the gelatinous envelope, but are not represented in the figure.

b. Vertical section of the yolk or ovarian ovum of the frog which has been hardened in alcohol, showing the germinal vesicle within and the canal of the yolk which leads down to it from the upper or germinal pole. The external line indicates the vitelline membrane.

c. Diagrammatic representation of the same section, showing, according to the views of Ransom, the relation of the canal or depression of the yolk to the germinal vesicle. The micropyle, if it exists in these ova, may be situated in the vitelline membrane immediately above this canal. This figure also shows the relations of the dark and light coloured parts of the yolk substance.

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* I have frequently observed this process, which has been beautifully described and figured by Mauro Rusconi in his work, "Amours des Salamandres Aquatiques, Milan, 1821."

† Entwickelungsg. der Geburtshoelferkröte, Solothurn, 1842.

It is towards the centre of the dark superficial part of the yolk that the first changes of embryonic development always take place; and it is apparent that this dark part corresponds more immediately to the germinal part of the yolk. It is beneath the central part of this dark covering that the germinal vesicle is situated in the ripe ovum. When taken from the ovary previous to impregnation, the ova float in water indifferently as regards the position of their parts; but after impregnation, when the imbibition of water allows of the free rotation of the yolk within its coverings, it is invariably found that the dark or germinal part of the yolk is directed upwards, and the whiter or grey spot downwards; — a circumstance by which the difference between the fecundated and the unfecundated ova may readily be detected. We may distinguish therefore, as the upper, dorsal, or germinal pole of the ovum, the central point of the dark part, and name the opposite point in the centre of the light-coloured space the lower or ventral pole.

The thickness of the dark layer of substance which covers the upper part of the ovum is throughout its greater part considerable; viz. about one-eighth to one-tenth of the whole diameter of the yolk. It thins off somewhat at its edges below. Within this darkest layer the colour of the yolk-substance is slightly shaded off into the grey substance of the interior: the consistence of the inner substance is less than that of the superficial layer, and it contains a cavity situated considerably nearer the upper than the lower surface of the yolk, in which the germinal vesicle is situated. This vesicle is not perfectly spherical in its form, but somewhat flattened from above downwards, and it is surrounded by a peculiar mass of fine granules.

The yolk-substance contains no cells nor large corpuscles; the greater part of it consists in the mature state of peculiar flat or tabular corpuscles, the largest of which are about $\frac{1}{2500}''$ in diameter. Most of these are quadrangular in shape, but somewhat rounded on the edges and at their angles. There are also numerous smaller particles of the same kind of every dimension from that already stated down to the smallest granules, and with some variation of shape, together with a considerable amount of molecules of very minute size, of which those in the darker part have the appearance of pigment granules. These last are accumulated in greatest quantity towards the surface; but they do not constitute a separate layer, being rather interspersed with the tabular corpuscles. There are also to be seen in the upper or germinal part a few rounded corpuscles, somewhat larger than the tabular particles, which seem to be formed by the aggregation of smaller molecules; but these have no external envelope nor clear nucleus, and only bear a distant resemblance to the cells which, after impregnation, are formed in the germinal part of the yolk-substance.

The peculiar quadrilateral tabular corpuscles refract light strongly, so as to present distinct outlines; they have also considerable firmness, resisting pressure, but by force may be broken up somewhat in the same manner as would occur in small plates of wax. From this circumstance they have generally been regarded as of a fatty nature, and were described by Vogt as stearine tables; but Virchow[*], from a careful investigation of their reaction with different substances, throws a doubt upon this view, and is more inclined to regard these corpuscles, both in Batrachia and in the ovum of the carp-fish, as composed of some albuminous or protein principle, the exact nature of which he has been unable to determine. He admits that they may also contain some oil. They are probably very analogous to the larger firm angular particles which were first described by J. Müller as forming the greater part of the yolk-substance in the Sharks and Rays, and which also exist in the ova of Cephalopodous Mollusca.[†]

The germinal vesicle of the Batrachian ovum is of very large proportionate size. According to Vogt, in the *Alytes obstetricans* its diameter is nearly equal to one-third of that of the entire yolk mass. In the common frog and toad it is somewhat less, but nearly $\frac{1}{40}$ of an inch. This vesicle may be obtained separate for examination by breaking open the yolk carefully under water; but it is much easier to observe its position, form, and structure in the ovum which has been hardened by some re-agent,—a plan which has been successfully adopted by a variety of observers. Cramer[‡] recommends for this purpose alcohol, or more particularly dilute chromic acid; Newport[§] employed alcohol, as I also have done with success; more recently Remak[||] states that he has found a mixture of a solution of sulphate of copper with alcohol, to which a few drops of rectified wood spirit are added, peculiarly fitted to give the proper consistence to the various parts, without inducing any destructive change in their structure or appearance. All observers agree that there is scarcely any other animal in which the relations of the germinal vesicle to the other parts of the yolk can be more favourably investigated.

The enclosing wall of the vesicle is of extreme tenuity, so thin, indeed, that some have doubted its existence. I have been able, however, to distinguish the double outline of its thickness with a good magnifying power of 350 diameters. The outer surface of the vesicle is not always of a regular circular or spherical form, but often presents within the yolk, both at earlier and more advanced stages, a notched appearance: when, however, the vesicle has been extracted from the yolk, I have generally found this appearance to be removed and perfect sphericity restored. It would appear also, from Vogt's observations in Alytes, that this appearance is not constant: it may depend on the viscidity of the contents, and the extreme softness and thinness of the enclosing membrane of the vesicle.

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[*] Zeitsch. für Wissensch. Zool. vol. v. p. 241.

[†] See J. Müller, über die Glatten Hai des Aristoteles, 1842, p. 36.

[‡] Bemerk. über das Zellenleben in der Entwick. des Früscheies, in Müller's Archiv. 1848, p. 20.

[§] Researches on the Impregnation of the Amphibia, First Series, in Phil. Trans. for 1851, p. 169. *et seq.*

[||] Untersuch. über die Entwickel. der Wirbelthiere, Berlin, 1855, p. 127.

It is only in the earliest stages of ovarian formation that any appearance of distinct maculæ, such as they have been described in other animals, is to be perceived; for from a very early period these spots or nuclei are already very numerous. As the ova approach maturity the contents of the germinal vesicle undergo very considerable and rapid changes, by which a number of corpuscles, some loose, others aggregated, and subsequently delicate cells, are formed, and completely fill the whole cavity of the vesicle.

The germinal vesicle is situated, in the ripe ovarian ovum, nearer the upper than the lower part of the yolk. When the egg has been hardened by the re-agents already referred to, there can be perceived in the middle of the upper surface, or exactly in the upper or germinal pole of the yolk, a minute depression, which was first noticed by Prevost and Dumas *, and which they, erroneously, according to most of the observers who have followed them, conceived to be connected with an aperture or pore in the external membranes of the ovum. Von Baer showed that this depression leads into a canal which extends from the upper pole of the yolk, through the yolk-substance, to the surface of the germinal vesicle. The existence of this canal has been fully established, and its situation well represented by Newport. The interval between the upper surface of the yolk and the germinal vesicle appears to become less as the ovum approaches maturity.

The vitelline membrane of the mature ovarian ovum in the frog is thin and homogeneous. In the ova which have escaped from the ovary into the abdominal cavity it is still so thin, that they are very liable to be broken by the slightest force applied unequally on their surface; but in their descent through the oviduct considerable consistence is given by the addition of the layers of albumen to the vitelline membrane. Besides the simple vitelline membrane, there appears to be a second envelope formed within the albuminous deposit. Remak †, indeed, describes the vitelline membrane itself as consisting of two layers, besides the superadded membrane within the albumen.

Formation of the Ovum, and Changes in its Progress.— The ovary of the Batrachia is peculiarly well adapted for making observations on the development of the ova, as the stroma is in small quantity and transparent, and as it contains at most seasons a considerable number of ova in different stages of their formation and progress. If examined in the autumn or in spring before pairing, there are generally found three sets of ova; one uniformly large and dark-coloured, obviously belonging to those which are about to be brought forth in the ensuing breeding season; another set, also of uniform size, but less than the first, and in which only a partial deposit of colouring matter has taken place, probably constitute the ova for the next season after the first; and, third, a number of ova of inferior magnitude to either of the other sets, and of most various sizes, down to the most minute, which we may suppose to comprise those destined for succeeding breeding seasons. It seems probable that three seasons are necessary for the full development of the ova in the common frog and toad.

The earliest ova are seen within the ovicapsules or ovisacs, in the delicate ovarian stroma; the more advanced are enclosed in their pediculated capsules or calyces.

The germinal vesicle is the part of the ovum first distinctly recognisable; but so soon as it, or any part of the ovum can be distinguished, the delicate membrane of the ovisac or ovarian follicle is also seen surrounding it. Leuckart * was never able to perceive a follicle without there being already also an ovum within it. It would appear, therefore, either that the follicle and germinal vesicle arise together, or that observations have not yet determined which of them has the priority. It has been stated by some, that in the very earliest periods a single macula or nucleus may be observed in the germinal vesicle †; but it is rare to find the germinal vesicle in this state, and I have generally observed the macula, even in the earliest stages, to be multiple, or to consist of several maculæ. Still it is undoubted that, in the earliest period, there are fewer maculæ than at more advanced periods, and that their number gradually increases. About the time of maturation of the ovum the contents of the germinal vesicle undergo further changes, to which reference will hereafter be made.

From a very early period, though perhaps not from the first, the germinal vesicle is surrounded by a thick viscid substance, which closely adheres to its surface. This substance is at first remarkably clear, especially at its outer part, where it has a hyaline appearance: a little later it becomes gradually more and more opaque, as if by the deposit in or mixture with its clearer substance of fine molecules or granules. This appears to be the primitive yolk-substance; which in these animals therefore, as in most others, is ascertained to consist of a clear basis or matrix, in which the granular part is suspended. The out-

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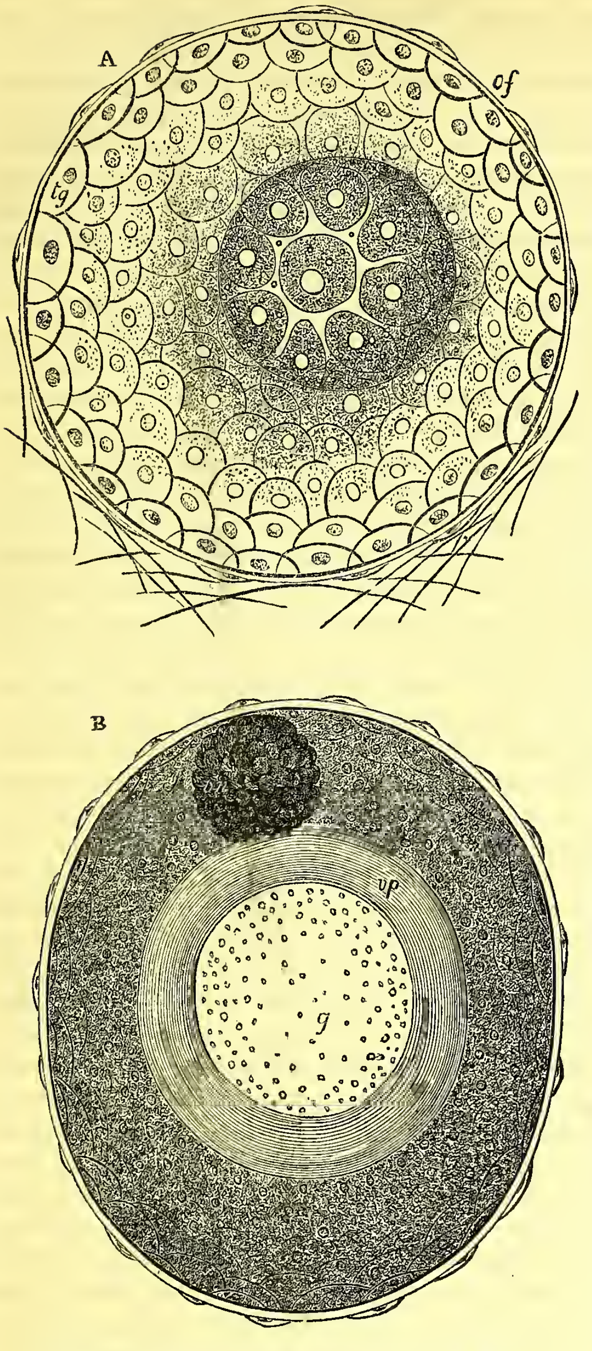
* 2me Mém. sur la Génération, &c., in Annal. des Scien. Nat. 1824, tom. ii. p. 104.

† Loc. cit. p. 127.

* Loc. cit.

† Mr. Newport describes the germinal vesicle of the frog's ovum as nucleated, even when half-grown. He also speaks of the corpuscles of the yolk substance as "nucleated cells" (1st Series, p. 176.); but this is quite inconsistent with the statements of most other observers.

Fig. 65 *.



Formation of the ovarian ovum in the Frog.

A, and B. Magnified representations of an ovarian follicle and its contents in an early stage of the formation of the ovum. The follicle is $\frac{1}{100}''$ in diameter: in A the follicular membrane and its epithelial lining are chiefly brought into focus; in B the parts of the ovum within are represented when the microscope was adjusted so as to place them in focus. The wall of the ovarian follicle consists of a structureless membrane or ovicapsule, and an external covering of thin flattened cells; the epithelial cells of the follicle within are seen in profile towards the margin, and full towards the centre (in A) where their granular contents and nuclei are distinct. In the centre of B the large germinal vesicle with numerous maculæ is seen; around it a clear space which is a part of the basement substance of the primitive yolk, and between this and the wall of the follicle there is seen superiorly the dark granular mass which has been called yolk nucleus. The clear primitive yolk is also surrounded by a finely granular vitelline substance which has begun to be deposited.

line of the clear part remains remarkably smooth and well-defined for a time, and there appears to be some fluid or different substance interposed between it and the inner surface of the ovicapsule. The homogeneous membrane of the latter is found at an early period to be lined by a single layer of very distinct largely nucleated cells, which lie flatly applied against its inner surface, but bulge or project roundly on their other sides towards the ovum. This layer of cells no doubt corresponds to the tunica granulosa of the ovisac in other animals, and has a similar destination.

There is as yet, neither in the earlier ova nor in those half-grown, any zona or other proper vitelline membrane; and it is obvious that what some authors* have described as such could be nothing more than the distinct surface of the primitive yolk. Whether this surface becomes condensed into a membrane, or at what time this may occur, has not yet been determined by observation.

Besides these parts in the early Batrachian ovum, there is another which has frequently been seen by various observers from Von Baer downwards, and which, as it is different from anything that has been observed in the ova of other Vertebrata, deserves some attention; I refer to a dark mass of granules situated excentrically or towards the side of the clear primitive yolk-substance, and between it and the tunica granulosa of the ovisac, and which, from its supposed connection with the formation of the yolk-substance, has been called the *yolk-nucleus*. This mass may easily be seen in ovisacs of the common frog of from $\frac{1}{150}$ to $\frac{1}{100}$ of an inch in diameter. It is then about one-tenth of the diameter of the ovisac. It is very opaque as compared with the other parts, being composed of aggregated heaps or small balls of finer granules. The opaque granules of the yolk have been supposed to be derived from this body, and it has been alleged that, as the yolk-substance increases, this yolk-nucleus gradually disappears or spreads itself round the germinal vesicle.† Leuckart, however, states that this body is not invariably present, and that it is subject to considerable varieties, and he is not inclined to attribute to it any important function in connection with the formation of parts of the ovum. I have in general found it present, and think it more probable that it may be destined to form the external and larger corpuscles of the yolk, while the clearer part immediately surrounding the germinal vesicle may contribute to the production both of these and of the finer substance in which the germinal vesicle is found imbedded. But farther observations will be required for the determination of these points.

As the growth of the ovarian ova proceeds, the deposit of fine granules in and around the primitive albuminous yolk-mass increases rapidly; and the yolk-nucleus, becoming less distinct, finally disappears at an early but somewhat variable period. The yolk-sub-

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* As Cramer, loc. cit. p. 21.

‡ See V. Carus in Zeitsch. für Wissen. Zool. vol. ii. p. 103.; and Ecker in his new edition of R. Wagner's Icones Physiolog. descript. of Tab. xxiii.

stance contains at first only fine granules; but in the second season of development there are found mixed with these, especially towards the surface, corpuscles of a somewhat larger size, and these are gradually converted into the quadrilateral tabular particles. The distinction of colour between the surface and the deeper parts, and between the upper and lower portions of the yolk, also now appears; but it is not till the third season of development that, along with a proportional enlargement of the yolk, the darkest kind of pigment is deposited among the corpuscles on the upper surface. The gradual extension of this coloured layer over a greater portion of the surface of the yolk from the upper towards the lower part has already been stated. The extent of the coloured portion marks in fact, in a great measure, the proportion which the immediately germinal part of the yolk bears to that not concerned in the first process of embryonic development; or it indicates at least the extent of the yolk which is immediately involved in the process of segmentation.

The vitelline membrane, I have already said, is absent during the early stages of development of the ovum; it appears to be present in the third season, but I have not been able to determine precisely its mode of origin. Farther observations are still necessary to ascertain whether, as in Mammalia and some other animals, a zona is formed by the condensation of the outer part of the primitive yolk-substance, or whether this membrane proceeds from another source. From the gradual flattening and disappearance of the inner cells of the ovarian follicle, and the close adhesion of their remains to the vitelline membrane in the later stages, I am led to believe, that the covering with which the yolk leaves the ovary may owe its origin to the amalgamation of one or more layers of fused or united cells of the tunica granulosa, or to the union of these with the zona or primitive vitelline membrane, should such exist.

There is no true cellular yolk, but the granular yolk is of proportionally large size; and if we are disposed to regard the yolk as containing both a formative and nutritive part, these are united or combined in a more close manner than in the larger ova of ovipara. The ova of Batrachia differ, on the other hand, greatly from those of Mammalia in their relation to the Graafian follicle; more especially in the fact of the ovum completely filling the follicle, and the entire absence, excepting in the epithelial lining, of fluid or other deposit between that layer and the surface of the ovum. The history of development shows that the peculiar structure of the ovum of Batrachia, as well as that of osseous fishes, has some connection with the large proportion of the yolk which becomes immediately germinal, and with the comparatively early period of advancement at which the young leave the egg and assume an independent mode of life.

Before concluding this account of the ovum of the Amphibia, it will be proper to notice the changes that have been observed in the germinal vesicle near the time of the discharge of the ova, and in its descent through the tubes till its exclusion. All observers are agreed that the germinal vesicle is no longer visible in the excluded ovum, whether fecundation shall have occurred or not; and the solution or disappearance of this vesicle is now looked upon, in these as well as in other animals, as a natural concomitant of the maturation of the ovum independently of fecundation. The recent and very precise observations of Newport* have shown, that in a considerable number of the ova about to leave the ovary but still situated within that organ, the germinal vesicle has disappeared, and that it is invariably gone in all those which have passed into the abdominal cavity.

Very shortly before disappearing, and when the ovum is approaching maturity, a remarkable change has been observed in the contents of the germinal vesicle; which is of great interest, in consequence of its probable intimate relation to the process of segmentation and cell-formation, which follow fecundation and are the precursors of true embryonic development. These changes have been described first by Cramer, and afterwards by Newport; the latter author, apparently, not having been aware of the observations of the former.

In early spring (February) Cramer† found the fine granules into which the maculæ of the germinal vesicle had previously been resolved by multiplication, beginning to unite together into heaps or small masses; and somewhat later he found these masses to become surrounded by a fine membrane or envelope, giving them all the appearance of small cells with a granular nucleus. There are often several hundred such cells at this period in the germinal vesicle of the brown frog, varying slightly in size and shape. At a still later period the greater part of the granular nuclei or contents of these cells become dissolved, leaving only a few remaining in each; and finally these also disappear, so as to render the cells entirely clear.

Now, all observers are agreed, that in the yolk-substance of the ovarian ovum, previous to the rupture of the germinal vesicle, there are not to be perceived any other solid particles excepting those already mentioned, viz., granules or heaps of granules, and the peculiar quadrangular tables; but many observers have perceived that immediately after the disappearance of the germinal vesicle, and during the whole time previous to fecundation, as well as after that change, the yolk-substance contains, mixed with the darker corpuscles, other clearer and spherical vesicular globules, somewhat larger than the tabular corpuscles. Vogt described them as scattered through the whole of the superficial yolk-substance in the *Alytes obstetricans*, and Cramer pointed out that these vesicular corpuscles are identical with the cells which he had observed to be formed in the germinal vesicle immediately before its

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* Researches, &c., 1st Series, p. 177.

† Müller's Archiv. 1848, p. 23.

disappearance. He attributed their origin, therefore, to this source ; and regarded it as probable that these cells, which may perhaps be descendants of the original maculæ of the germinal vesicle (but this is a point which he leaves undetermined), constitute afterwards the nuclei round which the tabular and granular substance of the yolk group themselves; and thus probably form, subsequent to segmentation, the nuclei or foundation of the cells which are the seat of true embryonic development.

Newport's description of these changes differs somewhat from that of Cramer, but is not altogether at variance with the view now suggested as to the nature of the process with which they are connected. He states *, that towards the period of maturity he found the germinal vesicle filled with secondary cells, and that each of these contained other or tertiary cells within them, and in the interior of these last were granules which he called quaternary. "In the midst of these numerous cells, and in the centre of the germinal vesicle, I was able to distinguish," says he, "in some specimens, one or two cells of larger size than the rest, and which I regarded as the remains of the germinal spot or central nucleus." He further states †, that these internal cells were, he conceived, afterwards thrown loose by the solution of the parent cells.

As to the mode of disappearance of the germinal vesicle, Von Baer had stated ‡ that, it gradually rises from its deeper situation, towards the surface of the yolk, and that, finally bursting or being dissolved there, its contents are allowed to flow over the surface of the yolk. This process he also described in several other animals as proceeding in a similar manner; and he supposed that the germinal substance from the vesicle was thus diffused over that part of the ovum which is most closely related to the subsequent changes of development. He regarded the canal of the yolk as the remains of a passage through which the vesicle had been carried to the surface. Newport, on the other hand, is quite confident that no such passage of the vesicle to the surface occurs in the ova of Batrachia, and that the vesicle most probably dissolves or disappears in its situation below the germinal part of the yolk. From the facts he has pointed out, Newport infers that the germinal vesicle is burst or destroyed by the development of the progeny of cells within it, and that the cells thus set free are mingled with the rest of the yolk. It belongs rather to the history of the changes which the ovum undergoes after fecundation, than to our present subject, to trace the relation between the cell progeny of the germinal vesicle now described, and the cells of embryonic formation afterwards developed ; but it may be proper here merely to mention that from the concurrent testimony of several observers, it seems probable that the origin of the blastodermic cells is closely connected with a combination of the vesicles or cells from the germinal vesicle with the other solid elements of the yolk-substance. To this process of cell formation the change of segmentation seems, in the Batrachia, as in all other animals, to be the necessary prelude.

It may be proper here also to state, in conclusion, that Newport has shown that the process of segmentation begins by a fissure which passes in a determinate direction through the canal of the yolk.

Although the statement of Prevost and Dumas as to the existence of an aperture in the membranes of the ovum, through which they supposed the spermatozoa might be introduced in fecundation, has not yet been confirmed by subsequent observers, but has on the contrary, met with an explicit denial from Von Baer, Newport, and Remak, after a very careful examination by these authors ; and although it would appear, from Newport's statement, that the spermatozoa penetrate the vitelline membrane of the frog's egg over a considerable portion of its surface, yet the discoveries which have in the last few years been made as to the existence of the micropyle in fishes and some other animals, are of so unexpected a kind, that we must not regard this point as altogether settled. Dr. Ransom, indeed, in some observations communicated to me, has stated his belief that a micropyle may still be discovered in the membrane of the Batrachian ovum. The statement of Prevost and Dumas on this subject is so precise that it deserves to be recorded in their own words. — "On remarque ensuite qu'il existe au centre de l'hémisphère brun une tache circulaire très regulière, jaune, et marquée d'un point opaque dans son milieu. Celuici provient d'un petit trou dont les deux membranes sont percées, ce qui met à découvert la bouillie brune que renferme l'ovule. Pour s'en assurer il suffit de vider l'œuf et d'examiner à la loupe les membranes transparentes qui sont restées intactes dans toutes leurs parties, sauf l'endroit qu'on a piqué pour évacuer la pulpe qu'elles contenaient." *

The observations of Von Baer, Rusconi, Newport, and myself have shown that with certain differences in the form and structure of the external membranes, the colour of the yolk-substance, &c., previously referred to, the structure of the ovum, and the phenomena of change at the time of its discharge, are essentially the same in the Newts as in the common Frog.

A few observations which I have made on the Menobranchus lateralis and Siredon mexicanum, show that the Perennibranchiate Amphibia agree very closely with the

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* Loc. cit. p. 176.

† Loc. cit. p. 177.

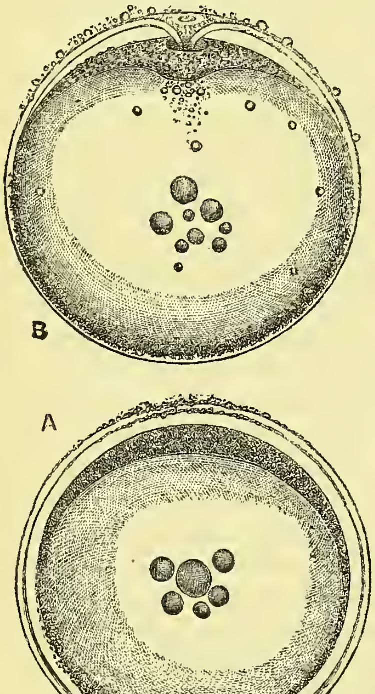
‡ Epistola de Ovi, &c., Fig. xxv.

* See Deuxième Mémoire sur la Génération :— Développement de l'œuf des Batraciens, &c., par MM. Prevost et Dumas, in Annal. des Scien. Nat. tom. ii. 1824, p. 104.

Salamandrina in regard to the structure and formation of their ova.

Osseous Fishes.—The ovarian ova of Osseous Fishes, while they bear a general resemblance to those of Vertebrata, among which they come nearest to those of Batrachia, are distinguished by several marked peculiarities. They are of middle size, and possess a strong external covering formed within the ovary. The yolk-substance contains several kinds of elements ; and the germinal vesicle is of considerable size. The external membrane is thick, strong, and elastic, and of a peculiar porous structure. The yolk-substance contains a large quantity of clear fluid, in which the albuminous granules and yolk corpuscles and the oil globules are suspended, the latter usually of large size and few in number; the germinal layer or disc is limited to a part of the yolk, varying in size from about a sixth to a half of the circumference, and the process of segmentation in this part after fecundation is consequently more limited than in Mammalia and most Batrachia; but more extended than in birds or scaly reptiles. The germinal vesicle contains subdivided or multiple maculæ. I now proceed to give a few details with respect to these several parts of the ovum.

Fig. 66 *.



Ovum of the Gasterosteus at the time of impregnation. (*From Ransom.*)

A. An ovum of the Stickleback eight or ten minutes after impregnation, showing the clear respiratory space formed immediately upon the access of spermatozoa between the external membrane and the surface of the yolk. Towards the upper part of the figure the situation of the micropyle is indicated by the small projections in the external membrane; towards the same or upper part of the yolk the germinal disc or layer is easily distinguished from the clearer part of the yolk; and in the middle a few large coloured oil globules.

B. The same ovum about three minutes after impregnation, showing somewhat in profile the funnel of the micropyle descending into a depression on the upper surface of the germinal part of the egg. In consequence of impregnation, however, the funnel of the micropyle has begun to rise out of the hollow, and the respiratory space to be formed by the separation of the external membrane from the surface of the yolk.

The yolk-mass or yolk-substance consists, in the more mature ovarian ova, of three parts : viz., the clear fluid, which is in great abundance and occupies chiefly the centre and the lower part of the ovum; the superficial layer of fine granules, with the vesicular corpuscles; and the large oily globules, which from their less specific gravity are usually situated towards the surface and on the upper side. In a number of fishes the clear fluid, which has an acid reaction, becomes immediately turbid or quite thick by the deposit of granular substance when water is added to it. This change is very apparent in the ova of the trout or salmon, which, when placed in water, retain their natural clearness and colour so long only as the coverings are entire ; but immediately on their being divided so as to allow of the action of water on the contents, the whole yolk is suddenly precipitated as a thick and somewhat tenacious granular mass. The albuminous matter which surrounds ova that have been spawned has an alkaline reaction. It is an interesting fact, that in these ova, when imbibition of water takes place as a consequence of fecundation, no precipitate follows ; but that in unfecundated ova left for some time in the same circumstances without fecundation, though unbroken, turbidity ensues; so that by the difference of internal appearance the fertile ova soon come to be easily distinguished from those which have not been fecundated.* The solid elements of the yolk-substance appear to be in general of three kinds for some time before the ovum has arrived at maturity : viz., 1st, a quantity of small granules comparable to the granular yolk-substance of the primitive ovum ; 2nd, collections of clearer vesicles and globules interspersed with the first, and in general partly mixed with them and partly situated in a deeper layer; and, 3rd, the large oil globules. These last are usually somewhat coloured ; they are comparatively large, and in some fishes are very few in number, and even reduced at last to only one, which is then of proportionally large size. In all fishes, the number of oil globules appears from the observations of Retzius gradually to diminish as the ova approach maturity.† The large oil globules float quite freely in the fluid of the yolk; so that from their greater lightness they always rise towards the side of the ovum which is turned uppermost; but the other elements of the yolk-substance, and especially the small granules of the germ-disc, come in the mature ovarian ovum to occupy one side of the yolk, and, as they form a coherent layer, do not move readily from this place. The smaller granular particles become more and more circumscribed in a layer on one side of the egg as it approaches maturity, so as to form a germinal disc; and this occurs independently of fecundation.

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* See a paper by Dr. Davy in the Proceed. of Roy. Soc. of Lond. 1852, p. 149.

† See Retzius in Müller's Archiv. for 1855, p. 34.

The germinal vesicle is not easily perceived in the ovarian ovum when it has attained some size. This proceeds in part from its extreme delicacy and transparency, and also from the opacity of the granules of the yolk within which it is situated. But it is to be observed also, that it disappears proportionally sooner than in other vertebrate animals. It is of considerable size in proportion to the rest of the ovum, having a diameter not unfrequently of $\frac{1}{50}$ or $\frac{1}{60}''$ in ova of $\frac{1}{20}''$. It is never to be found in ova that have left their capsules in the ovary; and according to Léreboullet's* observations in the pike and perch, it has already disappeared for a considerable time before it attains complete maturity. In the earlier stages of the growth of the ovum the germinal vesicle contains numerous distinct maculæ; but in the progress of development these multiply to a great degree, so that the vesicle is at last completely filled with fine clear cells, or brilliant vesicles, and extremely minute granules. When the vesicle bursts, its contents are dispersed over the yolk, and very probably are mingled or combined with the layer of germinal granules; but it is not probable, as Léreboullet supposes, that the whole of the formative layer of the germ (afterwards undergoing segmentation) is produced from the effused contents of the germinal vesicle. This multiplication of the maculæ and filling of the germinal vesicle with fine cells appears to be of an analogous kind to that which has been described by Vogt and Newport in the Batrachia; and it seems not improbable that in both classes of animals the dispersed maculæ may in some way or other, not yet fully ascertained, contribute to the origin and development of the blastodermic cells in the formation of which the process of segmentation results. It appears certain at least that, after the disappearance of the germinal vesicle and the dispersion of its contents, a marked change takes place in the disposition of the germinal part of the egg by its granular disc or layer becoming more circumscribed and distinct; and, as Léreboullet supposes, it may then be mingled with the brilliant points which proceed from the contents of the germinal vesicle.

The process of segmentation, into the description of which it is not intended at present to enter, is co-extensive with the granular layer or germinal disc of the ovum. The larger yolk globules and the fat cells are not immediately concerned in this process.†

The membranes of the ripe ovarian ovum of osseous fishes have been described by most recent observers as two in number; viz. 1st, the external tough membrane which some have called chorion or shell-membrane, and others vitelline membrane, which possesses a peculiar structure, hereafter to be described more particularly; and, 2nd, an extremely delicate film of membrane lying close to the yolk-substance and destitute of visible structure. The latter of these membranes is just discernible in the ovarian egg at the later periods of its growth; but in ova of two thirds their full size I have failed to perceive it. Dr. Ransom has observed, that in the Stickleback, Gasterosteus aculeatus, this membrane becomes more distinctly marked off from the substance of the yolk subsequent to impregnation, and that it follows the inflections of the surface of that substance during segmentation; from which he infers, that it is not to be compared with the vitelline membrane as heretofore described by authors in the ova of other animals. The observations which have been obligingly communicated to me by Dr. Ransom leave no doubt as to the existence of this inner membrane, and have shown the new and interesting fact that it is possessed of some vital contractile power. It seems probable that it proceeds from a consolidation of the outermost layer of the basement or clear substance of the yolk, in a manner somewhat analogous to the zona pellucida. But I refrain from saying more of it at present, as Dr. Ransom will ere long probably communicate his observations to the public in detail.

The external membrane of the Fish's egg which has been deposited in spawning or has been extracted from the ovary when approaching maturity, presents a remarkably well defined line internally, and is also generally smooth on its outer surface. In some fishes, however, as the perch, it is covered externally with villous, reticular, or other appendages, which serve to connect the ova in masses or strings, in the same manner as occurs with the albuminous matter added to the ova of some Batrachia, but in a less degree. In other instances, as the Stickleback, these villi or projecting processes are limited to one portion of the exterior. This membrane possesses considerable thickness and tenacity, and usually gives the ovum a nearly regular spherical form when imbibition is complete, as is the case after impregnation. Previous to that change, however, the outer covering of the Fish's egg is more yielding, and possesses so little elasticity, that it usually retains dimples or impressions made upon it from without. Two peculiarities of structure have been observed in this membrane which both merit farther attention, and one of which is of great interest.

The first of these to which I will refer is the dotted or porous structure of the external membrane. Von Baer* had remarked that the external membrane of the ova of the Cyprinus genus was not entirely homogeneous, but was marked through its thickness with fine lines set perpendicularly to the surface. Vogt observed a similar structure, and described it more fully in the Salmonidæ.* More recently attention has been particularly called to it by the fuller description of the structure of the egg coverings in the Perca fluviatilis by Professor Müller of Berlin. In this fish Müller described the radiated lines as produced by fine tubes which pierce the whole thickness of the external membrane, beginning with cup or funnel-shaped dilatations on the exterior, preserving a nearly equal diameter throughout, and terminating on the inner surface.† The tubes have a slight spiral winding as they pass through. That they are really hollow tubes Müller ascertained by finding that he was able to press portions of the coloured oily contents of the yolk through them. Müller farther observed, that in the perch each tube is set in a small prism, which terminates by a hexagonal end on the outer surface. According to Dr. Ransom's observations, however, it appears that the structure described by Müller in the perch is peculiar to that fish, and belongs only to an outer covering superadded to the surface of the dotted membrane, which last resembles in all respects that of other fishes. This outer covering appears to be of cellular origin; and Dr. Ransom thinks it may be due to the separation of the tunica granulosa along with the ovum. The diameter of these tubes in the perch is about $\frac{1}{10000}''$. In most other fishes the fine lines which appear to be tubular are much smaller. I have observed them in several fishes, and have rarely found more than ten of these tubes in the breadth of $\frac{1}{1000}''$, and the tubes themselves or double lines bounding them were not more than $\frac{1}{25000}''$ or $\frac{1}{30000}''$ in breadth. In looking at the flat surface of the membrane the ends of these tubes give the appearance of a finely dotted structure to the membrane. It is quite possible, however, even where they are finest, to perceive the circle or lumen of the tube by using a high magnifying power; and I have thought that I could also in the salmon perceive a hexagonal marking of the intervals between the pores (see *fig.* 68* D); but in this fish the size of the pores is only a third of that of the tubes in the perch as described by Müller, and the structure must be of a different kind according to Ransom's observation. All recent observers have recognised this structure in the external membrane of the fish's ovum. Müller conceived that the tubes he had observed in the perch might be connected with the introduction of the spermatozoa into the ovum; but Dr. Ransom does not find these tubes to pass entirely through the outer membrane of the perch's ovum, and has observed that the part of the true vitelline or dotted membrane which admits the spermatozoa is destitute of the additional layer; and it will immediately be shown that in all fishes a special and more direct passage for the admission of these bodies through the dense membrane is provided, constituting the second peculiarity of structure in the covering of the Fish's ovum before referred to.

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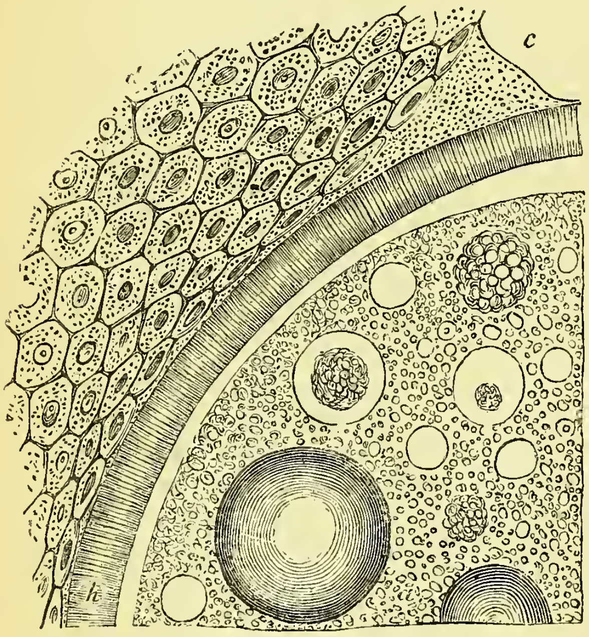
* Resumé d'un Travail sur l'Embryogénie du Brochet, de la Perche, et de l'Ecrevisse, in Annal. des Scien. Nat. 1854, tom. i. p. 237. *et seq.*

† M. Coste (Comptes rendus, 1850, vol. xxx. p. 692.) has described the germinal disc as being formed only after fecundation; but from the observations of Vogt, Aubert, Léreboullet, and Ransom, it is ascertained that it exists previously.

* Entwickelungsgesch. der Fische, Leipzig, 1835.

Fig. 67 *.



Part of the ovarian ovum of the Salmon.

Semi-diagrammatic view of the section of a portion of the yolk, porous membrane and external layer of cells in an ovarian ovum of the salmon of $\frac{1}{40}''$ in diameter. *a*, portion of the yolk substance showing the various granules, granular and nucleated corpuscles, and oil globules composing it; *h*, section of the porous or dotted external membrane; *c*, portion of the outer surface of the same turned towards the observer so as to show the punctated or dotted marking produced by the external apertures of the fine canals which run through the membrane; *d*, the flat surfaces of the nucleated cells (epithelial or granular) which line the ovicapsule, between which and *h* they are seen edgeways lying close along the outer surface of the dotted membrane; a granular or dotted appearance in the contents of these cells seems to indicate their conversion into the dotted membrane, which is probably formed in successive layers from the exterior. The diameter of these cells is $\frac{1}{1250}''$, that of their nuclei $\frac{1}{3300}''$.

The interesting discovery of an aperture in the external membrane of the ovum of osseous fishes is due to Dr. Ransom of Nottingham, who observed it first in two species of Stickleback or Gasterosteus, and afterwards in other fishes. This author made the farther interesting observation in the first-mentioned fish, that in impregnation the spermatozoa entered the ovum only through this aperture or micropyle. As this is the first instance in which the existence of this aperture and its relation to the process of fecundation have been ascertained by direct observation in a vertebrate animal, I will describe it more fully from Dr. Ransom's paper to the Royal Society of London*, and from farther information which he has obligingly furnished to me in private. I may also mention that I have fully confirmed Ransom's observations as to

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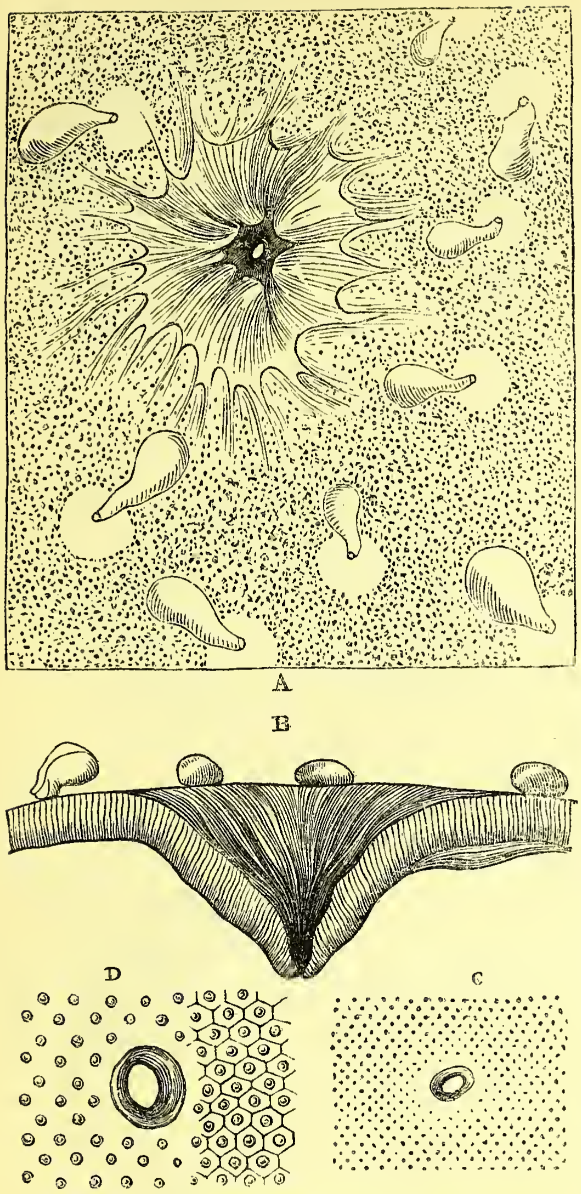
* Embryogénie des Saumons, Neufchatel, 1842.

† Müller's Archiv. for 1854, p. 186.

* Proceedings of Roy. Soc. 1854, Nov. 23rd.

Fig. 68*.



Micropyle of the ovum in Osseous Fishes.

A. Enlarged view of a quadrangular portion of the surface of the mature ovarian egg of the Stickleback containing the micropyle from above. In the outer part of this figure the general dotted appearance of the membrane is seen, and here and there the pediculated flask-like processes attached to the membrane in this fish in the vicinity of the micropyle; the radiated shading represents the appearance of the funnel-shaped depression leading to the aperture of the micropyle, which is seen in the centre of the space it encloses.

B. Transverse section of the dotted membrane and funnel of the micropyle of the same egg somewhat more enlarged, seen in profile; the aperture of the micropyle is seen towards the point of the funnel. This view is semidiagrammatic, and the fine canals passing through the membrane are represented fewer and wider than they are in nature.

The diameter of the whole ovum was about $\frac{1}{20}''$; the thickness of the external membrane $\frac{1}{1000}''$; the width of the base of the funnel about $\frac{1}{150}''$; the depth of the funnel $\frac{1}{200}''$; the diameter of the micropyle aperture at the apex $\frac{1}{3300}''$.

C. Small portion of the membrane at the apex of the funnel containing the aperture of the micropyle pressed flat, magnified 500 diameters; from the trout's egg.

D. A similar portion of the membrane magnified 1000 diameters. The lumen of the canals is seen, and an indication of hexagonal division of the spaces between them, represented somewhat too distinctly in the figure.

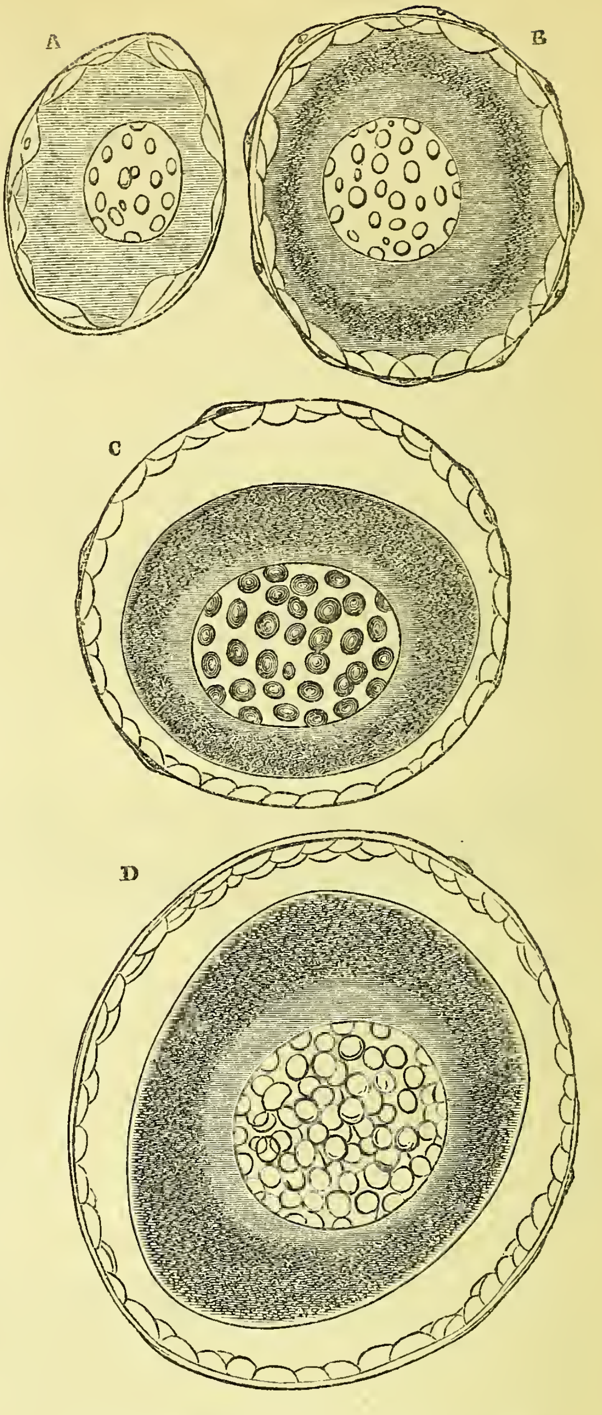
the existence of the micropyle in the ova of several fishes; and though I have not yet been so fortunate as to perceive the spermatozoa actually passing into the ovum through this aperture, the accuracy of Ransom's observations on this as well as on other points leave little doubt as to the fact stated by him.

The micropyle in the Gasterosteus, as described by Ransom and observed by myself, is a considerable funnel-shaped depression in the outer membrane, which projects inwards on the granular substance of the yolk, so as to indent this layer to some depth, and probably to reach near to the germinal vesicle, which lies imbedded within the germinal layer. The inner narrow end of the funnel terminates in a distinct rounded or elliptical mark, with a fine but distinct line bounding it, which has all the appearance of a foramen, and which is either an open passage or one which is closed only by an extremely delicate structure. The funnel-shaped depression leading to the micropyle may be easily seen on the surface of the egg of the salmon or trout when slightly dried of the adhering moisture, and is of such a size that it may be perceived with the naked eye or with a lens of low magnifying power. In order to perceive the micropyle itself, however, or pore in the point of the funnel, it is necessary to remove from the egg that portion of the dotted shell membrane containing the funnel; and having freed it from the adherent granules of the yolk-substance by careful washing, for which Ransom has recommended a solution of acetate of potash, this part of it may be viewed under pressure with great ease with a magnifying power of 200 or 300 diameters. The porous structure of the membrane is then seen to continue very nearly up to the margin of the micropyle. This last has a diameter of from $\frac{1}{3000}''$ to $\frac{1}{6000}''$. The appearance of a double outline surrounding the micropyle proceeds from the circumstance that, in looking through the funnel we see at once two portions of the narrowing wall of the passage of different widths.

In Ransom's experiments, very soon after spermatic fluid was placed in the water round the ovum of the Stickleback, several of the spermatozoa were perceived to pass in at the micropyle; and immediately upon this water was imbibed, and the space named the respiratory chamber was formed between the yolk surface and the external membrane; a change which in this fish did not take place in the unfecundated ova, but which in some others occurs without impregnation. It is from this fact apparently that Ransom is inclined to the opinion that the micropyle may be closed by a very delicate membrane, which in fecundation is removed or broken through by the entrance of the spermatozoa; but with regard to this point there is still some uncertainty. The germinal vesicle previous to its disappearance is imbedded below the superficial layer of yolk-substance in a stratum of granular matter; and Ransom conceives that at the time of the rupture of the vesicle, this granular matter being mingled with the contents of the vesicle, the more immediately germinal part of the egg is formed from the mixture of the two. However this may be, it seems not improbable, from the observations now referred to, that the spermatozoa are conveyed directly to the germinal part of the egg by the funnel of the micropyle. I shall afterwards have to state the more numerous instances in which, following its first discovery by J. Müller in the Holothuria, a micropyle has been detected in the ova of Invertebrate animals; and I may attempt to show the great importance of this aperture in connection with fecundation in ova with thick external coverings to which the spermatic substance does not gain access till the later periods of their formation. The accompanying figures of the micropyle in the Stickleback will give a sufficiently clear view of this remarkable structure. At present it may be permitted to remark that, if we consider the size of this aperture, and the ease with which it may be found in the ova of fishes by an observer whose attention has been called to its existence, together with the fact of its having been so long overlooked previously, there is much ground for caution as to negative statements as to the existence of a similar aperture in the ova of other animals. I have already made allusion to this subject in the previous sections, in which I have stated that Dr. Ransom has expressed to me his firm conviction, founded on observations, that the micropyle exists also in the ova of Batrachia. At the same time it is quite probable that such an aperture may only exist or be required for the admission of the spermatozoa when fecundation is of late occurrence, and when the covering membrane of the ovum is so dense as to resist the penetration of the spermatozoa through its solid substance.

It is right also to mention that the existence of this aperture, or rather the funnel leading to it, did not entirely escape the observation of preceding physiologists. The accurate Von Baer, in his work on the development of Fishes*, has described in the Bream (Cyprinus blicca) a funnel-shaped depression of the external membrane, which reached nearly to the surface of the germ; and he observed that this funnel was effaced as soon as the imbibition of water took place. He considered this aperture as most probably owing to the escape of the germinal vesicle from the surface of the yolk and through the coverings of the ovum, in the same manner as he had described in the frog†, and did not therefore conceive it to serve any immediate purpose in connection with the introduction of the spermatozoa. Dr. Ransom has observed that the effacement of the funnel which he had seen in the Stickleback is not invariably the consequence of fecundation in the Fish's ovum; for in the salmon and trout

Fig. 69.*



Development of the ova of Gasterosteus.

A. B. C. D. Four ova of the Stickleback in the earlier stages of their development within their ovisacs.

In that figured at A, which is the earliest, $\frac{1}{400}''$ in diam., the germinal vesicle placed near the centre has scarcely any perceptible membrane or wall, but resembles a gelatinous mass in which the small number of maculæ are developed: there is as yet no yolk, but only a slightly turbid fluid substance filling the space between the ovisac and the germinal vesicle: delicate epithelial cells project from the inner surface of the ovisac.

In B. $\frac{1}{250}''$ the maculæ have increased in number, the germinal vesicle, as well as all the other parts, has increased in size, the fine granules of the yolk substance have begun to be deposited towards the periphery, but there is as yet no vitelline membrane. The wall of the ovisac is now more distinct, and besides the internal cells, there are seen on the exterior the nuclei of external flattened cells.

In C. $\frac{1}{180}''$ the maculæ have become more numerous and distinct; the yolk granules are more opaque and in greater quantity, and the mass of the yolk more circumscribed, a clear space now intervening between it and the wall of the ovisac.

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* Entwickelungsgeschichte der Fische, Leipzig, 1835, p. 9. figs. 1. and 2.

† De Ovi Mammal. &c., pl. xxv.

he found the funnel-shaped aperture to remain for some time after the completion of fecundation, and in none of the fishes he has observed does he conceive the aperture of the micropyle to be closed.

The ova of osseous fishes appear to take their origin within the rudimentary follicles or ovisacs of the ovary much in the same manner as those of the Batrachia. The earliest part of the ovum that can be distinctly seen within the follicle is a vesicle of about half the diameter of the primitive follicle itself. A little later this vesicle is seen to be surrounded with a clear, jelly-like substance, in which some small dark granules are deposited chiefly towards the surface of the vesicle. There is as yet no enclosing membrane, but the follicle is seen to be lined by a layer of extremely delicate hyaline cells, often difficultly perceptible. The earliest recognisable part of the ovum, therefore, is the germinal vesicle; which, as in other animals, has soon deposited round it the clear gelatinous basement-substance of the yolk, in which the opaque yolk granules soon make their appearance. There is not at first any vitelline or other membrane enclosing the primitive parts of the egg, and indeed it is a considerable time before any such membranes are formed. The deposit of vitelline granules increases rapidly, so as to give the yolk considerable opacity; afterwards larger globules appear, and seem to increase by endogenous multiplication.* The oil globules are at first small, and equally diffused through the whole yolk; it is only in the later stages of formation that they unite into fewer and larger globules.† The granular or primitive yolk-substance continues to surround more immediately the germinal vesicle till the period when this vesicle is ruptured, and is probably spread over the germinal disc of the egg. Similar granules also occupy, however, in a layer the surface of this part of the egg previous to the rupture of the germinal vesicle; so that it is not probable that the germinal disc owes its origin, as Coste states ‡, entirely to the effusion of the contents of the germinal vesicle.

The ovum receives its firm porous membrane while within the ovarian capsule, but only in the latter part of the time of its formation. This membrane lies very close to the inside of the ovisac, is at first comparatively thin and destitute of apparent structure, and gradually increases in thickness towards the time of its approach to maturity. At the same time a remarkably thin pellicle may be distinguished close to the surface of the granular yolk-substance, scarcely meriting the name of membrane. As already remarked, it is difficult to determine what is the true homological signification of these membranes. The inner one might by some be regarded as a representative of the zona pellucida, or a consolidated pellicle on the surface of the yolk, though it must be admitted that Ransom's observation, that it follows the segmentation, is opposed to this view, and makes it more probable that it is only a part of the yolk itself. The origin of the external porous membrane I am inclined to connect rather with the interior of the ovarian follicle; but whether by exudation from it, or by amalgamation of the innermost layer of epithelial cells of the follicle, I have not yet been able to determine. I am inclined to regard the latter as most probable, and that this is the true vitelline membrane.

The manner in which the micropyle takes its origin has not yet been ascertained. It will afterwards be shown, that in a considerable proportion of those invertebrate animals in which this aperture in the egg coverings is found, it has existed from a very early period, and proceeds from the remains of the pedicle by which the ovum is originally connected with the ovarian substance. Such a pediculated connection has certainly not yet been observed by most of those who have investigated the ovarian ovum of fishes.* Rathke, indeed, observed the appearance of the remains of a pedicle in the detached ova of the Blennius viviparus †; according to Ransom the micropyle in the Pike is not a depression, but projects from the surface like a trumpet-shaped process; and in the earliest stage of development of the ovarian ovum of Trigla hirundo, according to Leydig ‡, the shape is somewhat pyriform or pediculated, in the same manner as in some of the invertebrate animals.

On the other hand, Ransom expressly states that he has never been able to observe the slightest connection in Gasterosteus between the pedicle of the ovum by which it is attached to the ovary, and the micropyle. This aperture he says is always situated at that side of the ovum towards which the germinal vesicle and the germinal disc are placed; but these parts have no regular connection with the pedicle. The pe-

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In D. $\frac{1}{140}''$, although the number of maculæ has greatly increased by endogenous multiplication, the germinal vesicle has not now undergone an enlargement proportional to that of other parts of the egg and ovisac: the granules of the yolk, especially towards the surface, are much increased, and a narrow clear marginal space on the surface now indicates the commencement of the formation of a zona or vitelline membrane. This appearance is also slightly perceptible in *fig.* C.

The dimensions of the several parts in these different specimens were as follows:

	A.	B.	C.	D.
Ovisac - -	·0025	·004	·0056	·007
Yolk - -	—	—	·0042	·005
Germinal vesicle -	·001	·0016	·0025	·0026
Maculæ - -	·00015	·00018	·00025	·0003

* Lereboullet, loc. cit.

† Retzius, loc. cit.

‡ Hist. gén. et part. du Développ. des Corps organ. tom. i.

* The pedicle here spoken of is not that of the ovarian capsule containing the ovum, but of the ovum itself within the capsule.

† Abhandlung. zur Entwick. part. ii. p. 4.

‡ Müller's Archiv. for 1854, p. 376. fig. 6.

dicle, he affirms consists only of the ovarian structure, and of no part of the membranes of the ovum. From his observations on Gasterosteus, in which the projecting bodies from the porous or outer membrane in the vicinity of the micropyle enable this part to be easily recognised, he feels confident that if any pediculated connection had existed it could hardly have escaped notice.

When the ovarian ovum has attained maturity it falls into the cavity of the ovary, or that which may be regarded as ovary and oviduct united, by the rupture of the ovarian capsule in which it is contained. The walls of the ovi-capsules have by this time become extremely thin; but according to Von Baer a small stigma or non-vascular mark may be distinguished where the rupture takes place. After the ova have fallen into the common cavity they are surrounded by a considerable amount of secreted albuminous matter, by which in some fishes the ova are covered when excluded. In some this albuminous secretion serves to unite the spawn in chains or networks. In other fishes the ova are covered externally with villous projections; but the manner in which these are formed has not yet, so far as I am aware, been observed.

One of the most remarkable, but as yet quite unexplained, varieties in the external coverings of the ovum in one of the osseous fishes, is that discovered and recently described by Ernst Hackel, as occurring in the family of Scomberesoces.* This consists in the formation, in the space between the surface of the yolk and the vitelline membrane (that is, the porous membrane), of a layer of long and very distinct fibres, which are wound somewhat spirally, but irregularly, over the surface of the yolk. Hackel has traced the gradual formation of these in fresh specimens of Belone from points on the surface of the yolk-substance; and in other genera he has observed several varieties in the forms of the fibres. They are on an average about $\frac{1}{3500}''$ thick, and long enough to surround the egg several times; and they appear to resemble the fibres of the elastic yellow tissue more than any other animal substance, but do not entirely agree with them. In the meantime we must suspend our judgment as to this very extraordinary addition to the surface of the ovum until farther observations shall have been made as to their distribution in various fishes or other animals, and as to their relation to the development of the embryo. †

Invertebrate Animals.—The ova of Invertebrata may be considered under two principal divisions, according as they present more of the large-celled or of the finely granular yolk-substance. The ova of the first kind are usually of a larger size; they possess a larger germinal vesicle, and often a divided or multiple macula; and the process of segmentation in them is either partial, that is, limited to one part of the surface of the yolk, or it occurs in a different manner on the upper and lower sides of the ovum. In these there is, in fact, nutritive as well as formative yolk. In the other division of animals the yolk is finally molecular, or is mainly composed of smaller granules, and is chiefly of the formative kind; segmentation usually involves the whole yolk, or if not so, is very nearly complete: the germinal vesicle is generally clear, and the macula most frequently single, and well marked. It is true that the form and structure of the ova of Invertebrata presents many and considerable varieties, as might indeed be expected among animals of such diversity of organisation as belongs to the great divisions of the Radiata, Articulata, and Mollusca; but still it is to be observed that as a greater degree of simplicity exists in the form and structure of the primordial elements than in the more developed textures and organs of animals, so also we find that much closer analogies may be traced among these elements in the lowest classes of the animal kingdom. We meet, therefore, with little difficulty, even in the most diverse tribes of the Invertebrate animals in tracing the correspondence of the essential parts of the ovum; and we are enabled also to trace a more close analogy between these and the corresponding parts in the Vertebrata than might have been expected. We are therefore warranted in applying to them similar designations; and we have daily increasing reason to trust to observations made on the ovology of the lower animals as the means of extending the knowledge of the reproductive functions in Vertebrata and in Man. Thus the recent discovery of the micropyle aperture in some animals, and the certain and clear observation of the penetration of the spermatozoa into the ovum in others, suggest novel and more general and extended views of the process of fecundation, and while they add certainty to the more limited observations of the same kind made upon animals higher in the scale, tend to prevent the adoption of partial views in regard to these functions of the animal economy.

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* Müller's Archiv. 1855, p. 23. See plates IV. and V.

† Some time after the above was in the hands of the printer, I received the first and second parts of the seventh volume of the Zeitsch. für Wissen. Zool., containing a notice of the discovery of the micropyle in the Salmo salar, and S. fario, by Professor Bruch of Basle. The observations leading to this discovery were made in the winter of 1854-5; and it is right to state here, that Dr. Ransom's discovery of the micropyle in the gasterosteus, which was communicated to the Royal Society on the 23rd of November, 1854, was made in the months of June and July previous; and these observations had been communicated to Professor Sharpey and myself in August and September. In the beginning of January, 1855, Dr. Ransom informed me by letter of his having found the micropyle also in the Trout, and a few days later in the Salmon. I then saw the micropyle in the ova of both of these fishes; and I have since examined it minutely in the Stickleback, and have confirmed in every particular Dr. Ransom's statements. The existence of the micropyle in these Vertebrate animals has thus been established by several independent observations; and I believe that no one who uses the proper means can fail to detect it in these and other fishes. Professor Bruch's observations were chiefly made on the ova after impregnation, which may explain the reason of his having failed to perceive the connection pointed out between this aperture and the depression in the centre of the germ disc. Bruch was like myself unsuccessful in perceiving the entrance of spermatozoa by the micropyle. His measurement of the micropyle in the Salmon and Trout does not agree with mine, making it much smaller.

It is principally among the more highly organised Invertebrata that we meet with that form of ovum in which the nutritive is combined in considerable quantity with the formative yolk, and in which segmentation is partial, such as the Cephalopoda, Insecta, Arachnida, Myriapoda, Crustacea, and some of the Articulate Worms. In by far the greater number of the Mollusca, such as Gasteropoda and Acephala, the ova belong to the smaller kind with more or less complete segmentation, as also in most of the Annelida, as Hirudinea and Lumbricina, the Nematoid, Cestoid and Trematode worms, with the Planariæ, the Rotifera, Echinodermata, Bryozoa, Acalephæ and Polypina.

I now proceed to give a short statement of the principal facts that have been ascertained as to the structure of the ovum in these animals, and to state some details with regard to some of those which are either best known or which present phenomena of the greatest interest.

1st. *Large-yolked Ova with partial Cleavage. Cephalopoda.*—The ova of this class of animals have already been referred to in connection with those of birds, scaly reptiles, and cartilaginous fishes, to which they present in some respects a greater analogy than to those of almost any of the Invertebrata. The considerable size of the germinal vesicle with its multiple maculæ, the large mass of the coloured yolk (nutritive), composed of conglomerated masses of yolk corpuscles, and the very limited extent of the process of segmentation, which affects only a round disc of the germinal part of the egg, are all characters in which the ova of the Cephalopoda, at least the Sepia and Loligo, which have been fully examined, are ascertained to be similar to those of the large-yolked group. We owe the most of our knowledge of the ova of this class and their development to Kölliker's interesting treatise, published in 1844.* The ova of the Sepia are deposited singly, but are attached in numbers close together by pedicles to the stalks of Algæ and other marine productions. Those of Loligo are arranged in small masses, in which a number are enclosed in a general bag or covering of gelatinous matter, which is attached along with others of the same kind by means of pedicles. I have found those of Sepiola also thus enclosed in small pyriform capsules.

The ovum of Cephalopoda possesses a firm laminated external covering or chorion, which in some is darkened on the surface by the colouring matter or ink, in others is transparent and colourless. Immediately within this outer membrane is situated a structureless vitelline membrane, containing the mass of yolk-substance, which is separated from the membrane by a slight interval. It appears to be ascertained that the chorion is formed by superposition on the surface of the ovum during its descent through the oviduct.

In the ovary the ova are contained in slender capsules, attached to the rest of the ovary by narrow pedicles. When ripe the ova escape from the capsules, in some species by an irregular laceration, in others by a more regular and defined opening, and, falling into the cavity of the ovary, pass thence into the oviduct, through which they are finally excluded. Fecundation is believed to occur soon after the escape of the ova from their ovicapsules or in the earlier part of their descent through the oviduct; but this process has not, so far as I am aware, been directly observed.

The ova of the common Sepia officinalis have an oval form, one end being much narrower than the other. It is at this the pointed extremity or narrow pole of the egg that the germinal vesicle is situated, while the egg is in the ovary, close under the vitelline membrane; and it is at this part also that, at a subsequent period, the process of segmentation and the first formation of the embryo take place. The narrow end is therefore the germinal pole. This extremity of the egg is always turned to the opposite side from the pedicle of the capsule, which is attached to the middle of the blunt or wider end.

One of the most remarkable peculiarities in these ova, is the extraordinary change which the outer part of the yolk and the vitelline membrane undergo during the greater part of the time occupied by the growth of the ovum in the ovary. This change, of which the appearance had been known to some previous observers, was first accurately described and explained by Kölliker. From his observations it appears that at first the ovarian ova are quite smooth on the surface, and that at the time of complete maturity of the ovum, or after its escape from the ovary, the vitelline membrane and surface of the yolk are also quite smooth; but that in the intervening time, that is, during the greater part of the period of its growth, the surface of the yolk is indented or marked with peculiar grooves, into which folds of the vitelline membrane pass so as to line them to the bottom, somewhat after the manner in which the pia mater descends into the sulci of the brain, but without the same convoluted form. This has been represented by Kölliker in the Sepia, and I have observed it in this genus, and have confirmed in every particular that author's statements as to this change. It appears that at first these inflections of the yolk and membrane begin as longitudinal folds, extending between the wide and narrow poles of the ovum, and, gradually increasing, become at last so deep as almost to meet each other in the interior of the yolk. Subsequently they are traversed by more numerous depressions.

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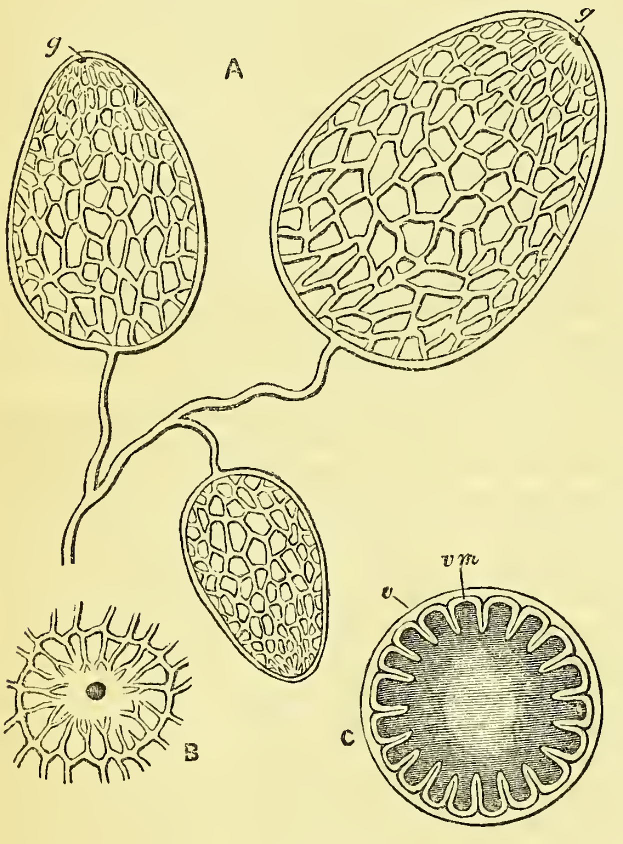
* Entwickelungs-gesch. der Cephalopoden, 4to. Zurich, 1844.

which subdivide them; and as these cross folds are formed the longitudinal ones beome gradually shallower. The surface of the egg then presents the reticulated appearance which is shown in *fig.* 70.* On making a section through such an egg, hardened in alcohol or any other suitable reagent, it is easy to perceive that the ovicapsule takes no part in the inflections, but that they consist entirely in the grooving of the yolk, and the corresponding bending into the grooves of the vitelline membrane. This state is maintained till the ovum is approaching maturity, when the depth of the grooves or folds speedily diminishes; and these come at last to be completely effaced in those ova which have left the ovicapsule. In Loligo, it is stated by Kölliker, there are only the longitudinal folds. No satisfactory opinion has been offered as to the cause of this peculiar structure.

Fig. 70 *.



Ova of the Sepia. (*From Kölliker.*)

A. Three ovarian ova of the Sepia in somewhat different stages of advancement attached by their pedicles to the ovary, and represented several times magnified. They all show the reticulated markings on the surface produced by the folding in of the vitelline membrane ; *g*, the place of the germinal vesicle and possibly also of a micropyle at the small pole of the egg, in which segmentation afterwards occurs.

B. Direct view of this germinal pole of one of the ova, showing the absence of the folds towards the centre in which the germinal vesicle is situated.

C. Cross section of one of the ova, showing at *o* the unfolded or smooth ovarian capsule, and at *v m* the folded vitelline membrane.

Towards the narrow pole of the ovum, the folds now described become less marked ; and they are entirely absent just at the pole itself, so that the germinal vesicle may be seen in the smooth space which is left between them. At this place I had some expectation to find an aperture of the nature of a micropyle ; and I accordingly sought for it in some specimens of the ovarian ova of Sepia which I had preserved in alcohol, but without success, perhaps on account of the opacity produced in the membranes by the alcohol, and the adhesion of the yolk substance to them. Professor Kölliker has since informed me that he believes the micropyle to exist in these ova, which I think extremely probable.

The germinal vesicle, according to this observer, remains entire and visible till the ova are mature, as may be seen by the examination of specimens hardened in alcohol. It disappears just about the time of the ova leaving the ovarian capsule ; but in several instances he found it still remaining in ova that were already free. It was always gone in those ova which had regained the smoothness of their exterior.

The yolk-substance of the mature ova consists entirely, excepting immediately at the seat of the germinal disc, of corpuscles somewhat similar to the vitelline tablets of the Frog's egg. At an earlier period there are heaps of fine granules of the same size, from which the corpuscles are therefore probably formed. In the earliest stage the vitelline substance is entirely composed of fine molecules — the primitive yolk — which appear to be formed in the same manner as in other animals.

The Cephalopoda furnish a remarkable example among the Invertebrata of a very limited or partial segmentation. This process, upon the detailed description of which I will not enter here, usually commences in a spot either in or more frequently near to the germinal pole, by the formation of the primitive groove which extends across the disc. The formation of the second groove, which crosses the first, the production of other radiating grooves, the separation of annular sets of segments from the periphery, and the successive steps of the process which follow, are probably determined by the same circumstances which have been referred to as related to this phenomenon in the cicatricula of the Bird's egg.

Gasteropoda.—In the greater number, if not almost all, of the remaining Mollusca, the ova differ greatly from those of the Cephalopoda, and approach more nearly to those I have classed under the groups possessing the small or middle sized yolk, which is principally or entirely formative, and which undergoes a more or less complete segmentation.* In the Pteropoda and in those of gasteropodous Mollusca, which have the male and female organs in the same individual, there is a remarkable combination of the ovary and testis in a single hermaphrodite organ, usually

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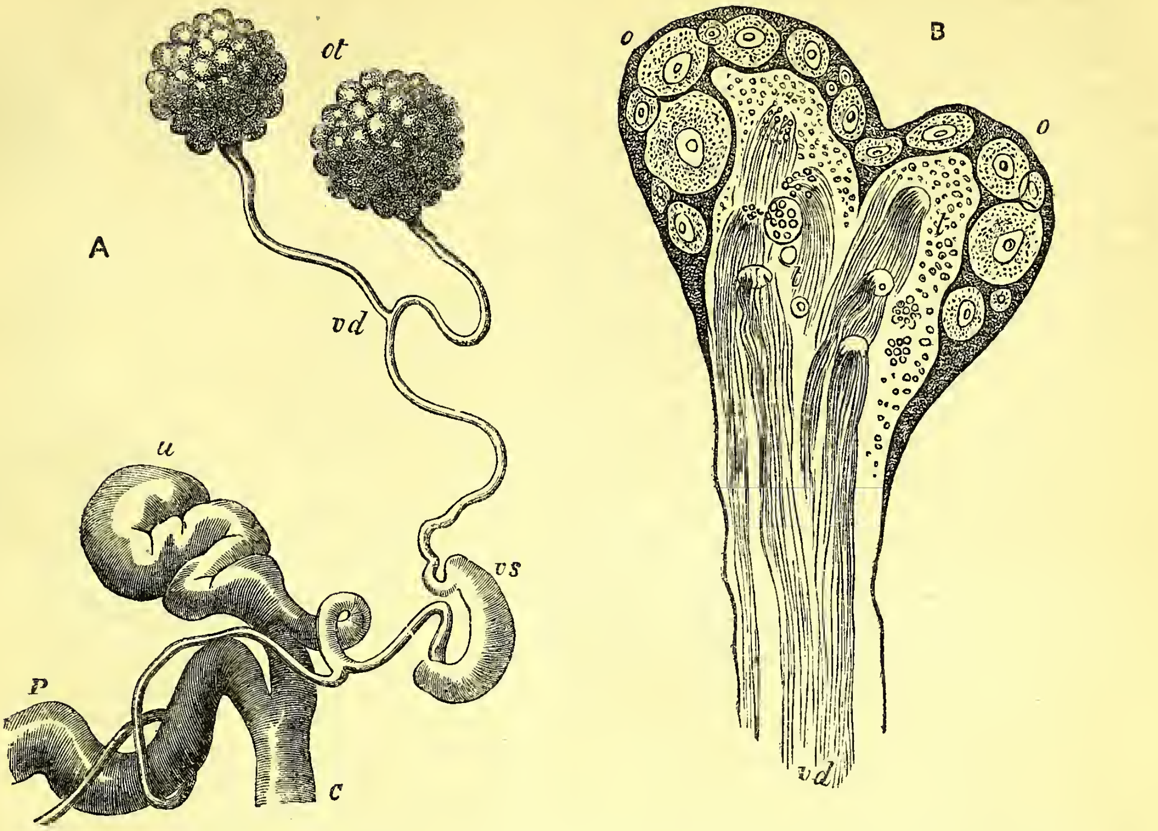
* The genus Sagitta, among the Pteropoda, is, however, probably an exception to this statement, as in it, according to Darwin, the embryonal part of the yolk is distinct from the rest, or rather covers it like a ring.

Fig. 71*.



Genital Organs of Phyllirhoe bucephalum, one of the Hermaphrodite Gasteropoda. (*From H. Müller and Gegenbaur.*)

A. The compound or hermaphrodite organs dissected out and represented several times magnified; *o t*, the two productive organs each composed of ovigerous and seminiferous parts; *v d*, the common excretory ducts for both kinds of organ; *v s*, the seminal vesicle; *u*, the uterus; *p*, a part of the penis; *c*, the common external vent.

B. One of the lobes of the common productive organ laid open and more highly magnified. Towards the surface *o o*, the ova are seen in different stages of development in the ovarian stroma; in the interior *t t*, the substance of the testis with spermatic cells and spermatozoa in various degrees of advancement; some of the filaments being very long; *v d*, the common excretory duct for ova and spermatozoa.

enclosed in the liver, the nature of which was for a long time involved in obscurity, and occasioned much doubt and difficulty to naturalists. The explanation of this peculiar structure we owe first to H. Meckel*, and Leuckart†; and more recently H. Meckel and Gegenbaur have described this organ particularly in one of the heteropodous Mollusca, viz. Phyllirrhoe bucephalum.‡ The outer part of this curious organ constitutes the ovary, the inner the testis; and the products of these respective organs, in leaving the seat of their first formation, pass together into an inner common cavity, and thence downwards in the excretory duct. There is, therefore, a common outlet for both. The ova and spermatozoa most frequently pass out at different times; but occasionally both these reproductive elements are seen together in the passages. It seems probable therefore that they in general meet for impregnation only in the lower part of the passages; but this apparently is not yet fully determined, and the modes of union may be various in different genera or families. At all events, the primitive ova and spermatozoa seem to come into contact with each other previous to the addition of the enveloping membrane.*

The ova of the Mollusca are in general of small size. The yolk consists of a viscid albuminous substance, containing suspended in it minute granules, and a variable quantity of coloured oil globules. The germinal vesicle is proportionally of considerable size; and the macula is distinct and granular. Leuckart† states that he and Nordmann have ascertained that in Lymneus, the first part of the ovum which is formed is the germinal vesicle, that the yolk-substance begins as a clear transparent albuminous matter surrounding the germinal vesicle, and, as we have seen in various other animals, the granular yolk matter is gradually deposited in this clearer part of the vitelline substance, occupying at first principally its outer part. The vitelline membrane does not exist at first, but seems to be formed at a later period by the consolidation of an external layer of the primitive yolk substance.

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* Müller's Archiv. for 1844, p. 483., see plates XIV. and XV.

† Zur Morphologie und Anatomie der Geschlechts Organ. 1847, p. 128.

‡ Zeitsch. für Wissen. Zool. vol. v. p. 355. pl. XIX.

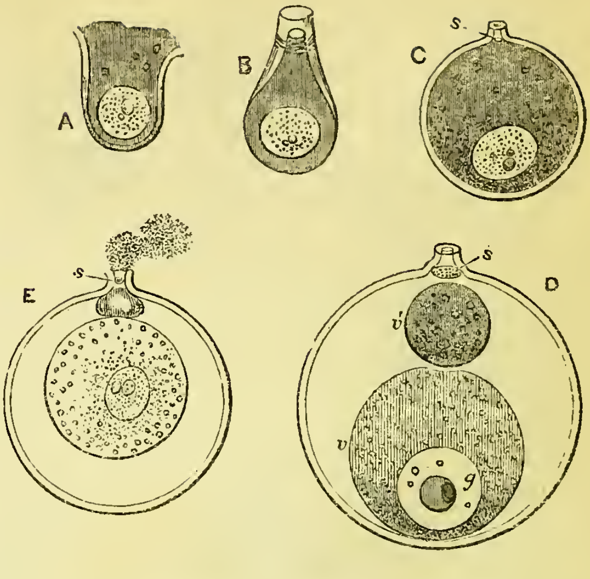
* The hermaphrodite gland exists in the Pteropoda, Apneusta, Nudibranchia, Infero-branchia, Tectibranchia, and Pulmonata. The Mollusca which have separate sexual organs belong chiefly to the orders Cyclobranchia, Scutibranchia, Tubulibranchia, and Cirribranchia, some Heteropoda, Pectinibranchia, and operculate Pulmonata or Cyclostoma.

† Article Zeugung, p. 800.

The time of the disappearance of the germinal vesicle has not been determined in many of these Mollusca. Previous to segmentation a phenomenon occurs, which has now been observed in a large number of animals, but which first attracted special attention in the gasteropodous Mollusca; viz., the separation of one or more clear hyaline liquid globules of considerable size from the surface of the yolk substance, into the space between it and the vitelline membrane. This was first observed by Dumortier[*], and described by Pouchet[†], by Van Beneden in the Aplysia[‡], by Nordmann in Tergipes Edwardsii[§], by C. Vogt in Actæon[||], and by various others. A precisely similar phenomenon has also been observed in some of the Vertebrata, as in Mammalia by Wharton Jones, Barry, and Bischoff, and in Batrachia by Newport. But though this separation of one or more hyaline globules from the yolk-substance at the time of segmentation appears to be a very general accompaniment of that process, it must be confessed that its import, either in connection with fecundation or development, has not yet been ascertained.

Acephala. — In Acephalous Mollusca the ova are generally of small size, the yolk-substance principally finely granular, the germinal vesicle clear, with a distinct macula, which last not unfrequently presents the form of a double or elongated biscuit-shaped particle. The vitelline membrane is distinct and possesses considerable strength; and there is generally a considerable space occupied by clear fluid between it and the surface of the yolk. The most interesting feature of the ova of these Mollusca is the funnel-shaped aperture which most of them possess, leading through the vitelline or external membrane into the space occupied by the yolk. This aperture, styled micropyle by J. Müller in the Holothuria, the first instance in which it was discovered, in 1850[¶], was observed in the ova of Unio and Anodonta by Leuckart[**] and Keber.[††] The latter author supposed that he had observed the penetration of a spermatozoon into the ovum through this aperture, and has described with great formality and minuteness all the phenomena which he conceived were related to that process. Although Keber was correct in asserting the existence of the micropyle in these Mollusks, it appears that the body described by him as spermatozoon cannot have been of that nature, seeing that it has been proved by other observers that the appearance on which Keber's supposition was founded existed long before fecundation, and remained long after the commencement of embryonic formation in the same condition.[*]

*Fig. 72 *.*



Ova of Unio in different stages of development.

(A. B. C. and D., *from Hossling*; E. *from Keber.*)

A. The early stage of the ovum, when the germinal vesicle alone is distinguishable lying in a bulging part of the ovarian substance.

B. The same somewhat more advanced; the ovicapsule and vitelline membrane have assumed the pediculated form, and the yolk granules surround the germinal vesicle.

C. The ovum now enlarged and spherical in form, the yolk granules increased in quantity, and the pedicle narrowed so as to form a short micropyle tube; *s*, the small body taken by Keber for a spermatozoon, existing long previous to the occurrence of fecundation.

D. The ovum, &c. at a later stage; *g*, the germinal vesicle; *v*, the yolk; *v'*, the separated portion of the yolk; *s*, as in C. now enlarged.

E. A nearly similar stage of the ovum as figured by Keber. Some of the contents of the separated portion of the yolk are escaping through the micropyle aperture; *s*, Keber's alleged spermatozoon.

The existence of a similar aperture or micropyle in several other Acephalous Mollusca has been ascertained by the recent investigations of various authors; but the actual entrance of the spermatozoa by the aperture, has not, so far as I aware, been satisfactorily observed. There seem, however, to be sufficient grounds for believing that in the Acephala, as in other animals in which it is found, the micropyle is immediately related to the process of impregnation, by affording a ready access of the spermatozoa to the yolk through the more resistent membranes of the ovum. The accompanying figures from Keber and his critic Hessling give a sufficiently clear view of the nature of this structure in the mature ovum of Anodonta.

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[*] Embryol. des Mollusques, in Annal. des Scien. Nat. for 1837, p. 136.

[†] Id. lib. for 1838, vol. x. p. 63. See also Pouchet's further observations in his work, Théorie positive de l'Ovulation spontanée, pl. XVI.

[‡] Annal. des Scien. Nat. 1841, p. 126.

[§] Id. lib. 1846, p. 147.

[||] Sur l'Embryol. des Mollusques Gastéropodes, id. lib. 1846, p. 33.

[¶] Archiv. 1852, p. 19.

[**] Article Zeugung, p. 801, Ann. 1853.

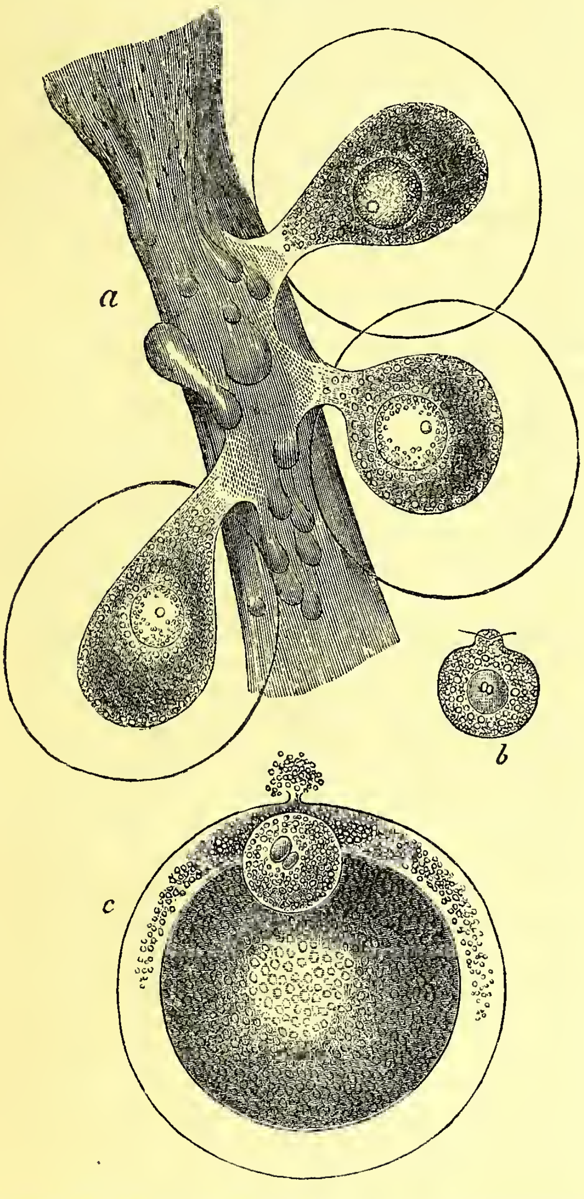
[††] De Introitu spermatozoorum in ovula, &c. Königsberg, 4to. 1853.

[*] Hessling, in Zeitsch. für Wissensch. Zool., 1854, vol. v. p. 380.; and Bischoff, Wiederlegung des von Dr. Keber bei den Naiaden, &c. Giessen, 4to. 1854.

In this family of Mollusca the micropyle forms a small but very apparent funnel-shaped projection from the surface of the outer membrane; and its hollow nature may easily be ascertained by the fact that the fluid and granular yolk-substance may be forced through it from within. The yolk ball is placed excentrically within the vitelline membrane, the inner surface of which it touches just at the place where the micropyle is situated.

From a variety of observations, it has been shown that the micropyle of the Acephalous Mollusca owes its origin to the early pediculated attachment of the ovum. This has been fully brought out by the observations of Hessling in Unio and Anodonta, of Leydig in Venus, and of Lecaze Duthiers in Cardium and some other genera.* From these observations it appears that the ova first arise in the ovarian stroma by the formation of the germinal vesicles, as in most other animals, each vesicle possessing a distinct single macula. These vesicles come very soon to be surrounded by some of the primitive or finely granular yolk, which gradually increases in quantity. These parts are from a very early period enclosed by a membrane which may be regarded as vitelline, but which is differently disposed from that in any of the animals previously referred to; for, instead of having a regular and complete spheroidal or vesicular form, this membrane is elongated at one part into a pedicle, so as to give the whole of the early ova a pyriform shape, and so as to attach them to the ovarian substance by the pediculated parts of the vitelline membrane. In Venus de-

Fig. 73*.



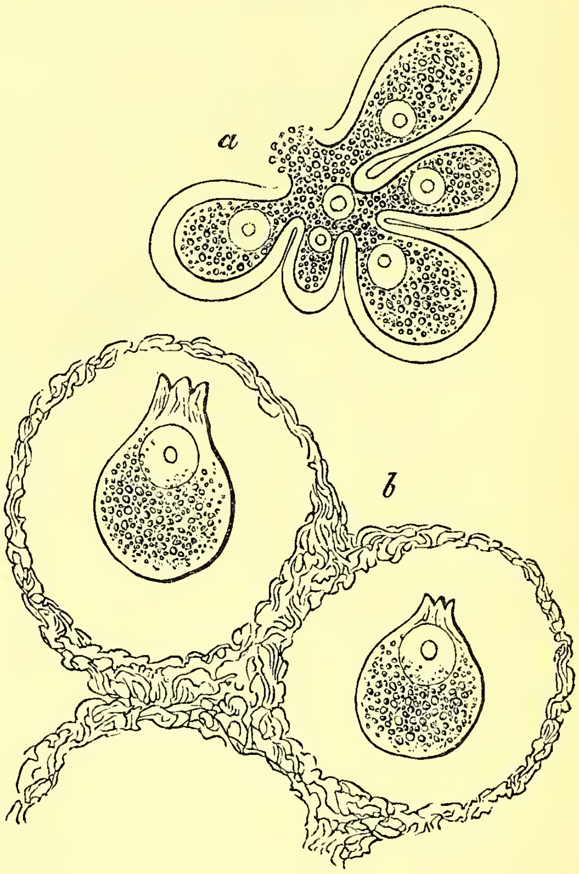
Structure and Formation of Ova in Acephala. (From Lecaze Duthiers.)

a. Portion of the ovary with three pediculated ovicapsules and contained ova from Cardium rusticum, magnified 400 diameters; the micropyle is afterwards formed at the place where the pedicles are detached from the secreting cœca of the ovary.

b. Unripe ovum of Spondylus gæderopus magnified 170 diameters, showing the remains of the capsule at the upper part, and the projection of the vitelline membrane at the same place where the micropyle is situated.

c. Ripe ovum of the same burst by pressure, showing the escape of some yolk granules through the micropyle and into the space between the yolk and the outer membrane. In this and the previous figure the double state of the macula is represented.

Fig. 74*.



Ovarian ova of Venus decussata. (From Leydig.)

a. A group of five ova in their earliest stage projecting from the ovary in their pediculated capsules: the germinal vesicles with single macula, the vitelline granules, vitelline membrane, and ovicapsule are all distinct.

b. Two ovicapsules within which at a more advanced stage the ova have become detached from their pedicles, the remains of which at the upper ends of the ova form the micropyle. A considerable amount of albumen has been deposited between the ovum and the ovicapsule.

* Annal. des Scien. Nat. 1854, ii. p. 155.

cussata, according to Leydig*, the ova are arranged in aggregated pediculated groups, from which it seems probable that they are originally produced in numbers by the multiplication or division of multiple germs, somewhat in the same manner as will afterwards be stated to have been observed by Meissner among the Gordian Nematoid Worms. An albuminous layer is afterwards formed externally, and may be instrumental at last, from its increasing thickness, in separating the ovum from its pediculated attachment to the ovary. There seems therefore to be little doubt that in these Mollusca, and in a certain number of other Invertebrate animals in which the micropyle has been observed, this apparatus is produced by the remains of an original or early ovarian pedicle. In the Unio and Anodonta it is certainly not formed by the peculiar process of development from within the ovum, which has been elaborately described by Keber.† It will afterwards be shown, however, as indeed may be concluded from what has already been stated in regard to osseous fishes, that in other animals the micropyle may arise in other modes and without the early existence of the pedicle now described.

When the ova are detached by the rupture of the pedicle in the Acephala, they lie, in different stages of advancement, but all provided with the micropyle, in the general ovarian cavity. The coverings of the Acephalous ovum appear to be composed at least of two layers, of which the inner may perhaps be looked upon as the vitelline membrane, the outer as a chorion; but sufficient data have not yet been furnished to determine the homological rank of these membranes. The early connection, in a pediculated form, with the ovarian stroma might point to a different view of their nature. Leydig states that while in Unio and Anodonta the albumen is deposited within the membranes, in Venus it is added externally. The micropyle appears to be closed previous to the commencement of embryonic development.

Arthropoda.—The ova of Articulate animals might with most propriety be classed with the large-yolked group, at least as regards the ova of Insecta, Arachnida, and the higher Crustacea. In addition to the germinal vesicle and finely granular yolk-substance, they all contain a large proportion of clear or oil globules of considerable size; and the process of segmentation is generally limited to a small portion of the yolk surface. The ova of these three classes present, however, many subordinate differences in their structure and mode of production, which renders it necessary to give a short separate account of them in this place.

Insecta.—The ova of insects are more especially distinguished by the extraordinary varieties of their external form and appearance. These varieties affect, however, principally, or depend upon modifications of the external covering, chorion or shell-membrane, as it has been called. They differ also from those of most other animals in a frequent departure from the regular symmetrical form. Some are nearly hemispherical, others more oval; many are somewhat bent in an antero-posterior direction*; many present the most curious elevations and irregularities on their external surface—reticulated ridges or fringes, and depressions, tubercles, hairs or spines, or other long processes, sometimes single, at other times in numbers. These modifications of the external coverings of the eggs of Insects appear to have reference chiefly to the protection of the ova from the effects of external injury, and to serve various mechanical purposes connected with their deposition and attachment; but they are not, in most at least, attended with any important varieties in the internal structure, which, on the whole, presents considerable uniformity throughout the whole class. The ova of all insects, we shall afterwards see, are provided with one or more apertures corresponding to the micropyle.

All recent observers agree that, in the ova of Insects, in addition to the external shell-covering, there is a delicate transparent vitelline membrane. The germinal vesicle is of proportionately large size. Its macula is at first single; but in the course of the growth of the ovum it becomes multiple, or diffused as a finely granular or molecular substance throughout the vesicle.† The germinal vesicle is situated in a vitelline or germinal area composed of fine granules, in which without doubt the limited process of segmentation afterwards takes place; but fuller observations are still much required in regard to the segmentation of the yolk in insects, which has as yet been very rarely seen. The germinal vesicle appears to be burst and diffused at a comparatively early stage of the growth of the egg.

The external membrane consists in general of more than one layer of substance. The outer and inner are described as being generally more clear, dense, and homogeneous; the middle one, in some insects at least, presenting greater varieties of structure, and not unfrequently being composed of united nucleated cells. It is in these several layers of the outer membrane that the micropyle apparatus, recently discovered, is situated. The existence of a micropyle in the ova of Insects was first published by Meissner, in September, 1854‡; but the discovery appears to have been made simultaneously by Leuckart, who has given a most interesting and elaborate description of this apparatus, and of the minute structure of the membranes, in a great variety of insects, in a memoir recently published by him.§

Meissner described several varieties of the

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* Müller's Archiv. 1854, p. 320.

† Hessling and Bischoff, loc. cit.

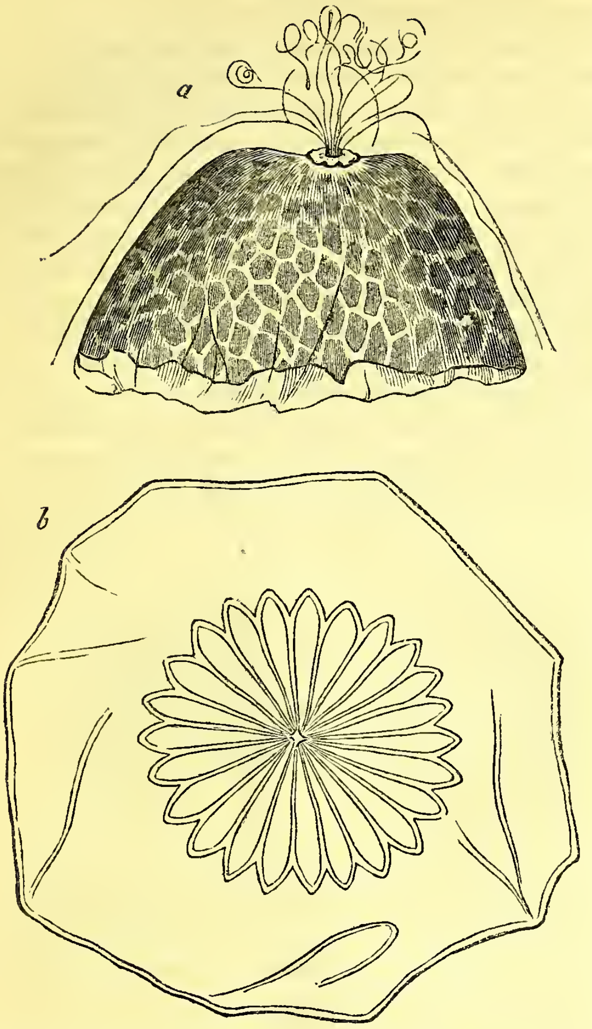
* This has reference to the position they occupy during their formation in the passages of the female parent.

† See R. Wagner's Prodromus Hist. Generat.

‡ Zeitsch. für Wissen. Zool. vol. v., p. 272.

§ Memoir on the Micropyle and Minute Structure,

Fig. 75*.



Micropyle in the ovum of Insects. (*From Meissner.*)

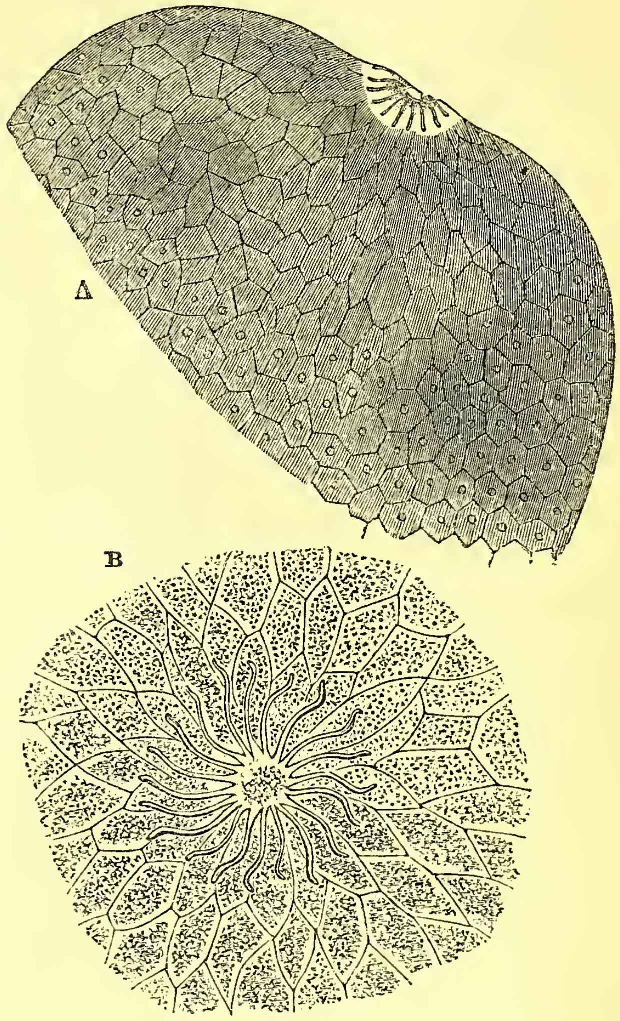
a. A portion of the upper pole of the ovum of Musca vomitoria from the Vagina. There are shown in succession the vitelline membrane, chorion and outer envelope, and at the upper part in profile the micropyle aperture situated in the middle of a nipple-like projection of the chorion, and with a number of spermatozoa involved in it.

b. Direct view of the upper pole of the ovum of an insect belonging to the Pyralida. The micropyle aperture is seen in the centre of the radiated markings of the chorion.

micropyle apparatus in the ova of Insects belonging to the following genera, viz., Musca, Tipula, Culex, Lampyris, Elater, Teleophorus, Adela, Pyralida, Tortrix, Euprepia, Liparis, Pieris, Panorpa, and in more than one species of several of these genera. The same author also observed and described in Musca vomitoria a number of spermatic filaments entangled in the micropyle.

Leuckart's observations, which are fuller and more minute than those of Meissner, and differ in some of their results from those obtained by that author, were extended over a very large number of Insects. Among nearly a thousand different kinds, he succeeded in detecting the existence of the micropyle in not less than two hundred; and his detailed observations on this apparatus, and the structure of the membranes, extend to one hundred and eighty species. This must furnish ample proof of the universality of the existence of the micropyle in this class of animals, when we consider the minuteness of the object and the difficulty of obtaining specimens in a condition suitable for the investigation. Leuckart has stated, indeed, that in all instances in which the ova were ripe and favourable for examination, he was enabled to assure himself of the presence of this apparatus.

Fig. 76*.



Micropyle of the ovum of Lepidoptera. (*From Leuckart.*)

A. Side view of the upper part of the ovum of Sphinx Populi, showing the micropyle, the radiated markings surrounding it, and the cellular and other structure of the coverings of the ovum.

B. More enlarged and direct view of the vicinity of the micropyle in the same. The dotted or punctated structure belonging to the chorion is here represented.

In a certain number of instances, amounting to about a dozen, Leuckart farther found that the spermatozoa adhere to the micropyle, and that a certain number of them pass into the ovum by this aperture. He observed that a

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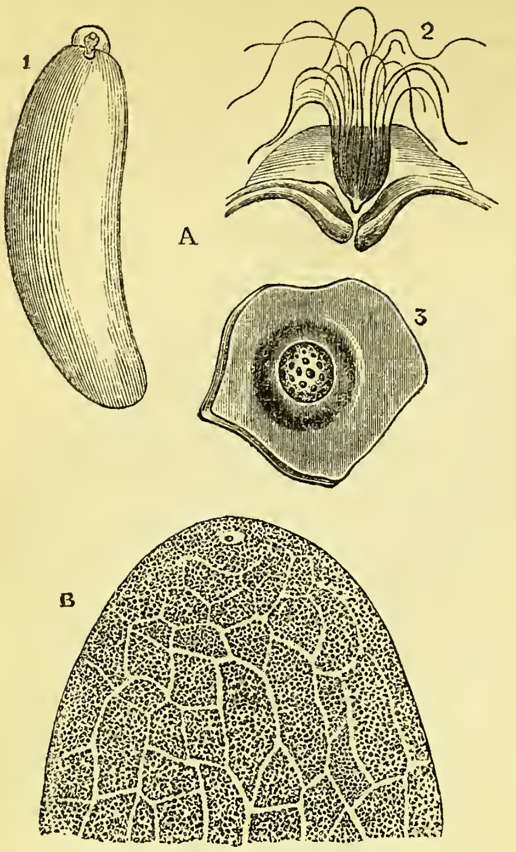
&c., of the Ova of Insects, chiefly pupiparous, in Müller's Archiv. Nos. 1. 2. and 3., February and July, 1855, p. 90., *et seq.*, with five plates, with 122 figures. There can be no doubt that both of these authors made the independent discovery of this curious structure. Perhaps the priority claimed by Leuckart, may be accorded to him, as he had previously stated the probability of its existence in his article "Zeugung," published in 1852, p. 906.

Fig. 77*.



Ovum and Micropyle of Dipterous Insects. (From Leuckart.)

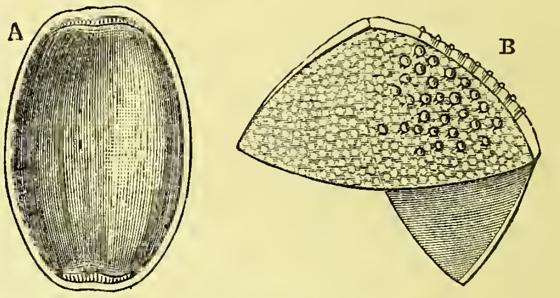
A. Ovum of Melophagus ovinus (Muscida). 1. The entire ovum, presenting at its upper part the adherent mass of spermatozoa close to the micropyle. 2. This upper part more highly magnified, showing a section of the micropyle, above which the point of the conical mass of spermatozoa glued together by an albuminous substance is inserted, while externally the filaments float free. 3. The micropyle apertures seen directly from above.

B. Side view of the upper part of the ovum of another insect of the same order, showing a single micropyle aperture and the dotted structure of the chorion.

small mass, formed of the spermatozoa which have met with the ovum in its descent through the female passage, comes to be lodged in the depression of the micropyle, and is fixed in that situation by a lid or covering of albuminous matter. It is somewhat remarkable that the greater part of this mass remains for a long time apparently without any change, even when embryonic development has advanced to a considerable extent; but he ascertained that a few of the spermatozoa belonging to the mass, usually not more than three or four, really enter the ovum and effect the change of fecundation. We are, however, as yet at a loss to conjecture what farther purpose may be served by the mass of persistent spermatozoa near the micropyle. Leuckart has also made the novel and interesting observation, that the depression and aperture of the micropyle become at a later period converted into a deeper funnel, which is connected directly with the mouth of the embryo, and undoubtedly serves, according to this author, to convey nourishment from without to the embryo. The head of the embryo lies, according to Leuckart and other observers*, in all instances, at that end or pole of the ovum which is uppermost in the oviduct, as may be most easily observed in ova of the cylindrical form, such as those of the common house-fly; but according to Leuckart, the micropyle is not, as Meissner had stated, always at that end, being sometimes at one, sometimes at the other, and occasionally at both poles. The provision for the escape of the embryo, however, is usually at the upper or anterior pole, while the lower or hinder pole more generally serves to fix the ovum, as it is often pediculated or otherwise modified in its form in connection with this purpose.

In some Insects, as is shown in the accompanying figure of the ovum in Pulex irritans, the micropyle consists of a number of foramina nearly of uniform size.

Fig. 78*.



Ovum of Pulex irritans. (From Leuckart.)

A. Entire ovum, magnified, showing the micropyle apparatus with a number of foramina at both poles.

B. Portion of the chorion with the micropyle foramina, more highly magnified.

In a previous part of this article allusion has already been made to the great facility with which the development of the ova of insects may be traced, in their successive stages, as they lie in different parts of the tubular ovaries and oviducts. According to the Interesting observations of R. Wagner †, the upper end of the fine ovarian tubes are filled with a number of germinal vesicles. Wagner supposed indeed that these were at first nucleoli or germinal maculæ, and that a vesicle was developed round each macula; but Leuckart‡ and Stein§ were never able to detect the germinal vesicles before they already possessed the macula. The primitive yolk arises as in most other animals—first, by the collection of a clear substance immediately round the germinal vesicle, and by the subsequent deposit in this matrix of the fine granules of the vitelline substance; later still the delicate vitelline membrane is formed, perhaps by the consolidation of a film of the primitive yolk-substance.

As the ova attain a larger size, each one being situated in the lower part of its compartment

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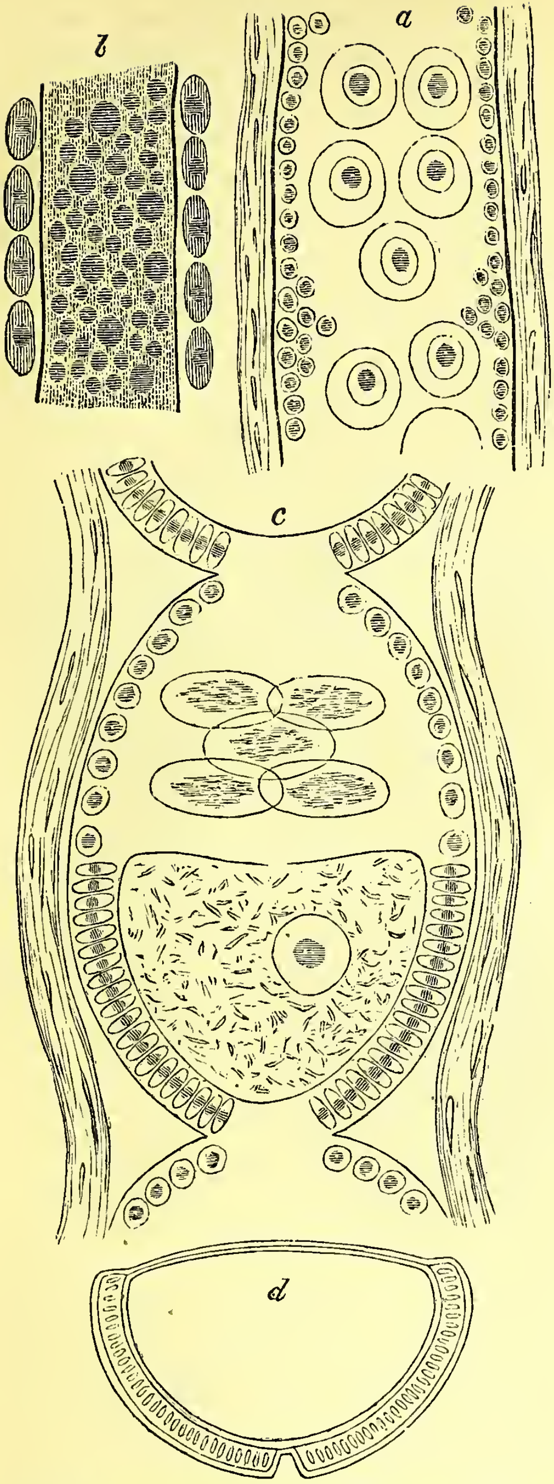
* See Kölliker, de prima Insector. Genesi, 4to. Turici, 1842.

† Prodromus, Hist. Gener. p. 9., and Beiträge zur Entwickel., &c. p. 42. See *fig.* 40. Append. of Cyclop. Anat. and Physiol.

‡ Zeugung, p. 803.

§ Vergleich. Anat. und Physiol. der Insecten, Berlin, 1847.

Fig. 79*.



Development of the ova of Lepidopterous Insects. (*From Hermann Meyer.*)

b. A small portion of the upper part of the ovarian tube from the larva of Saturnia Carpini. The entire lines mark the basement membrane of the tube; externally elongated epithelial cells are placed on it; internally a number of larger and smaller free nuclei are imbedded in an albuminous fluid.

a. A similar portion of the ovarian tube from Bombyx Mori more developed. The external epithelial cells are visible now only as elongated nuclei; a part of the internal cells now form a lining to the wall of the tube, while others of a larger size, which have become complete cells, towards the centre, form the primitive ova; of these last only a few undergo farther development.

c. One of the loculi or chambers of the oviduct of Hyponomeuta variabilis. The wall of the tube with its external epithelial nuclei as before, enclosing now the entire loculus and the small portions of the adjacent ones represented in the figure. The lower half of the loculus is occupied by the developed hemispherical ovum in which the several parts, viz. germinal vesicle with macula, yolk and vitelline membrane, are seen. The lining cells of the oviduct are seen to be elongated and modified in structure preparatory to their forming along with the albumen one of the external coverings of the ovum (chorion). In the middle of the upper half of the loculus there are the remains of five aborted primitive ova.

d. Section of the coverings of the ovum of Harpyia vinula, which may be taken as an example of the hemispherical ovum of Lepidopterous insects.

of the oviduct, there are to be seen in the intervals between the ova numbers of large clear globules or cells, which have been supposed to furnish the materials for the growth of the ovum ; but it appears more probable that these are merely abortive ova or germinal vesicles, which, though at first similar in size and structure to those which have been farther developed, have undergone a retrograde process, and are ultimately removed by absorption.

The production of the chorion or shell membrane does not take place till the ovum has attained nearly its full size. It appears to proceed in part from the consolidation, over the whole surface, of one or more layers of albuminous fluid secreted from the wall of the oviduct. But the observations of Hermann Meyer* have shown, in an interesting manner, that a part of the outer membrane is also derived from a conversion into it of the inner cellular or epithelial lining of the oviduct, at the place where it is in closest contact with the surface of the ovum. Many of the varieties in the appearance and structure of the external covering may probably depend on the different modes of development of these cells. As to the origin of the micropyle, it does not appear to proceed, as has been supposed by Meissner, from the mere deficiency of these cells in a certain space; and it is not dependent, either, on its pre-existence in the vitelline membrane. On the contrary, according to Leuckart, it is formed in the chorion before it appears in the vitelline membrane ; and it is not in any way connected with an early pediculated condition of the ovum, which, as is well known, never at any time exists in insects.

Before leaving the history of the ovum in this class, it may be proper to make the following addition to what was stated in an earlier part of the article in reference to the remarkable modification of the reproductive process, by which, in the Aphides and several other insects, many individuals are produced without the formation of true ova, or the concurrence of the two different sexual products. The learned editor of the American translation of Von Siebold's "Comparative Anatomy of the Invertebrate Animals," Dr. Waldo Burnett, has given, at p. 464. of that work, a short statement of his own observations on the origin and mode of formation of the repeated broods or colonies of Aphides, made on a large species of that insect, viz., A.

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* Zeitsch. für Wissen. Zool., vol. i. p. 190.

Caryæ, and of his views as to the nature of this process of non-sexual reproduction in general. The viviparous Aphides, according to Dr. Burnett, are neither male nor female, and do not possess, as has been supposed, any ovaries or oviducts. The new colony already begins to be visible within the body of its parent before the latter has itself been brought forth. The substance in which the new progeny takes its origin consists, at first, either of a single nucleated cell of $\frac{1}{3000}''$ in diameter, or of a small mass of these cells attached in the same place as that occupied by the ovary in the oviparous females. These masses increase in quantity, are subdivided by a kind of notching into more numerous masses; and each of these being inclosed in a capsule, the whole come to be arranged in a continuous row or series. There is not, however, any germinal vesicle nor segmentation, as in the sexual ova; and when development of the new insects is complete, it is by falling into the abdominal cavity, and by escaping through a genital aperture (porus genitalis) that the offspring is excluded.

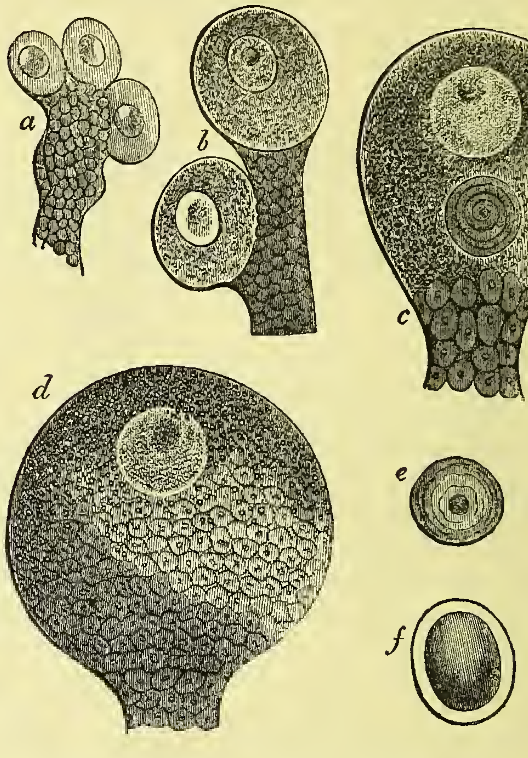
With regard to the origin of the cellular mass or germ from which the non-sexual progeny proceeds, Dr. Burnett states that a small mass, of a different appearance from the germinal part of the ovum, is seen to be included within the arches of the embryo; and the next colony is produced from this mass. He regards this process as analogous rather to one of internal gemmation than of true generation, coinciding therefore more nearly with the views of Leuckart and Carpenter than of Steenstrup and Owen.

Arachnida.—The ova of nearly all the higher Arachnida do not differ much in their internal structure from those of Insects; but they do not present the same varieties of external form. Their mode of first origin is also very different. All the higher Arachnida are, like Insects, of separate sexes. The Tardigrada are hermaphrodite; and in these as well as some other simpler Arachnida, as Pycnogonida and Acari, the ovum, though proportionally of large size, is of extremely simple structure, approaching very nearly to that of the lowest classes of Invertebrate animals.

The ova of the higher Arachnida are generally spheroidal; the chorion or external membrane is generally smooth; the vitelline membrane is slender, clear, and structureless; the yolk-substance is not unfrequently coloured, often purplish, consisting of a considerable quantity of large oily-looking globules, smaller granules of various sizes, and larger corpuscles which have been looked upon as cells, but which Leuckart states are only aggregated masses of granules held together by a viscid substance. The germinal vesicle is proportionally large, placed eccentrically, and possesses a macula, which in some genera is simple and flattened, as in the Scorpion, in others multiple and granular, as in Epeira.

The formation of the ova may be observed in Arachnida with great ease, from the manner in which they are disposed in the ovary, projecting like bunches of grapes from the central part of that organ, in almost every stage or degree of advancement. The process has been carefully observed by Wittich* and others. So soon almost as the ovum begins to be formed, it causes a bulging or projection of the membrane from the surface of the ovary; and when that has somewhat increased in size, the ova hang or project from the surface in small pediculated ovi-capsules. According to Wittich, V. Carus †, and Leuckart, the part of the ovum which earliest makes its appearance within the small ovicapsules is the germinal vesicle. At first it appears quite simple and without a macula, which last soon after-

Fig. 80*.



Ovarian ova of the Spider. (*From Wittich.*)

a. Small fragment of the ovary of Epeira diadema from which three ova project in the early stage of their development previous to the formation of the yolk: the germinal vesicles are enclosed in the membrane formed by the bulging out of the ovarian substance.

b. Two ova similarly situated, but more advanced; the primitive granular yolk substance intervening between the germinal vesicle and vitelline membrane.

c. An ovum still more developed; the germinal vesicle occupies the upper part; in the finely granular yolk substance below is seen the dark body regarded by some as a yolk nucleus, presenting an appearance of concentric lamellar structure; towards *c.* in the figure, or close to the connecting pedicle, the large nucleated cells are seen, which usually occupy that situation, and appear to give rise to the cellular yolk substance.

d. More advanced ovum greatly increased in bulk, the pedicle diminished, and the yolk completely occupied by the larger cells or corpuscles; the yolk nucleus has disappeared or is obscured.

e. & *f.* Different forms of the yolk nucleus or dark body, which for a variable time is placed within the ovum during its formation.

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* Die Entstehung des Arachnideneies im Eierstock, &c., Müller's Archiv. for 1849, p. 113.

† Zeitsch. für Wissen. Zool., vol. ii., 1850, p. 97.

wards appears as a small dot or nucleolus. The yolk begins, in the same manner as we have had occasion to state in many other animals, first by the clear deposit of a basement substance round the germinal vesicle, and the subsequent formation of opaque granules in it; the vitelline membrane is of later formation. As the egg increases in size, the larger corpuscles and the fat globules gradually appear. The ovarian ova of several spiders contain besides the usual parts another body of a peculiar kind, the nature of which seems still involved in some doubt. This body is eccentrically placed near the yolk mass of the primitive ovum, and is of considerable size, viz. about $\frac{1}{240}''$, of a yellowish colour, and, during the earlier part of its existence at least, consisting of concentric layers of a hard granular matter. V. Carus* has compared this body to the yolk-nucleus of the Frog's ovum; and both he and Von Siebold seem disposed to consider it as in some way or other the source of the granular substance of the yolk; but according to Wittich this view is not well founded, as he has observed the body remaining in the ovum till it reaches maturity, though it loses its concentric laminated structure, and becomes clearer and vesicular. Von Siebold, on the contrary, states that it gradually disappears. The large clear or oily globules appear, according to Carus, to be produced from near the pedicle of the ovum, at a place where there is fixed a group of cells apparently destined for their formation.

No observations have as yet been made, so far as I am aware, on the existence of a micropyle in the ova of Arachnida.

Almost all the Arachnida are oviparous. The Scorpions are an exception, however, bearing their young alive; and it is deserving of notice that in this family the embryo is developed in the ovum while it still remains in the ovary. In the greater number of this class embryonic development commences in a blastoderm, which covers only a part of the surface of the yolk, situated in what may be called its lower part or pole †; and the segmentation of the yolk is therefore limited or partial, as in Insects. In the higher Arachnida the steps of this process do not appear to have been yet satisfactorily observed. I may refer, however, to the researches of Kaufmann of Lucerne on the development of the Tardigrada, as affording clear and beautiful illustrations of the process of segmentation, which is shown to be complete in the lower Arachnida.‡

Crustacea.—All the animals of this class are of distinct sex; but in the allied Cirrhipedia hermaphroditism most frequently prevails. In some of the Cirrhipedes, however, it has been shown by Mr. Darwin § that the sexes are also distinct, as in some of the species of the genera Ibla, Scalpellum, Alcippe, and Cryptophialus. In these instances the males are very minute, and are attached, almost like parasites, to certain parts of the more developed females, the place of their attachment varying in different species. It is interesting to observe that these males, as in the case of several of the Epizoa, are often of the most rudimentary organisation.*

The ova of the greater number of Crustacea, especially the more highly organised genera, belong, like those of most of the Articulata, to the group in which a considerable amount of nutritive yolk is present along with the formative part, and in which the process of segmentation in the latter is partial. The formative disc is situated on the lower surface of the ovum; and from that part the development of the embryo emanates. Even among the higher decapodous Crustacea, however, the ova are of very various sizes †; and in the lowest genera, as among the Entomostraca, the ova are proportionally the largest, although they are of the simplest structure, and present the smallest amount of nutritive yolk; so that, in this as in other classes of animals, magnitude alone is no true criterion of the internal structure of the ovum.

The ova of this class have been described principally by Rathke ‡, by Erdl §, R. Wagner ||, Leuckart ¶, Leydig **, and others; but the knowledge both of their structure and their mode of formation is yet far from being sufficiently minute or complete. They present, indeed, many varieties, which renders it difficult to give any general description of them. The following may however be stated. The ova of Crustacea are often variously and brilliantly coloured. The yolk-substance consists of a large quantity of clear globules of considerable size, having the aspect of oil globules, in which the colouring matter chiefly resides. In some ova these globules attain the size of $\frac{1}{450}$ of an inch. There is also a more fluid granular matter in the yolk, and in the more mature ova there is a layer or disc of granular corpuscles on one side which afterwards is the seat of segmentation and embryonic formation. The germinal vesicle is of considerable size, in some instances possess-

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* Loc cit., p. 99.

† See the Researches of Herhold De Generat. Aranearum in Ovo, 1824; and Rathke, zur Morphol. Reisebemerkung. 1837; and in Burdach's Physiologie.

‡ Zeitsch. für Wissen. Zool., vol. iii., p. 220. See Plate vi., figs. 3. to 11.

§ Monograph of the Sub-class Cirrhipedia, &c., printed by the Ray Society, 1854, p. 27, &c.

* It is also a remarkable fact, pointed out by Mr. Darwin in his interesting Researches, that even among the hermaphrodite species there are sometimes distinct male individuals attached parasitically to the hermaphrodite animals; these have been called complementary males.

† Thus, for example, the ova of the river crawfish (Astacus fluviatilis) are twice as large as those of the common lobster.

‡ Entwickel. des Flusskrebses, 1829; in Burdach's Physiologie, vol. ii. 1837; in his Abhandl. zur Bildung und Entwickel. Gesch. &c., 1833; in Dissert. de Animal. Crustac. Generat. 1844; and various other treatises.

§ Entwickel. des Hummereies, 1843.

|| Prodrom. Hist. Generat., 1836.

¶ Article Zeugung.

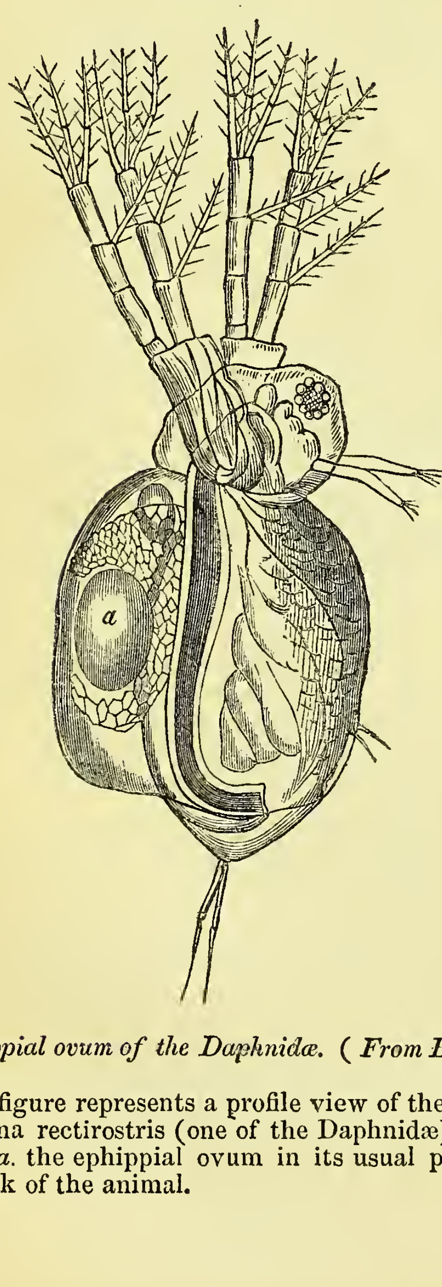
** On Argulus foliaceus in Zeitsch. für Wissen. Zool., vol. ii.

ing a single nucleus, in others multiple maculæ.

The formation of the ova may be observed with ease in any of the smaller isopodous Crustacea. According to Leuckart in Oniscus or Armadillo, it is essentially the same as in the Arachnida. The ova consist at first of germinal vesicles, originating below the epithelial lining membrane of the ovarian sac. The yolk-substance first appears as a clear deposit round each germinal vesicle ; minute opaque granules are then formed in this substance, and subsequently the larger albuminous and oil globules gradually make their appearance. The vitelline membrane, which is very delicate and structureless, is added at a comparatively late period, in the Oniscus for example, when the ova are about $\frac{1}{120}''$ in diameter.

In many of the Crustacea the ova also acquire a chorion or shell membrane of considerable strength. On arriving at the lower part of the female passages, the ova of many genera also receive an addition of a peculiar so-called albuminous secretion, which becomes coagulated in water, and thus, when the eggs are laid, serves to glue them together in heaps or to cause them to adhere to the hinder feet, caudal plates, &c., of the parent, where, as is well known, they remain during the whole progress of embryonic development. In the Monoculi and some other Entomostraca, there are marsupia or pouches appended to the genital orifices of the parent, in which the ova are retained during the formation of the young.

Fig. 81*.



Ephippial ovum of the Daphnidæ. (*From Baird.*)

The figure represents a profile view of the female of Moina rectirostris (one of the Daphnidæ) showing at *a.* the ephippial ovum in its usual place on the back of the animal.

In all the bisexual Crustacea the ova are fecundated while still within the body of the female parent ; but the phenomena and period of this process have not yet been acurately determined, partly perhaps in consequence of the peculiar form and motionless condition of the spermatic corpuscles belonging to the greater number of this class. No micropyle has yet been observed in the crustacean ovum.

From the observations of several naturalists it is now well ascertained that in the entomostracous Crustacea, there commonly occurs a production of young individuals without impregnation, somewhat in the same manner as previously described in the Aphides. " In the Daphnia," says Dr. Baird *, "it is now clearly ascertained that a single copulation is sufficient, not only to fecundate the mother for life, but all her female descendants for several successive generations ;" and it was considered probable by Jurine, that in some species this might extend to the fifteenth generation.

In the Daphnia and other similar Entomostraca, the ova are transferred from the ovary into a cavity situated below the shell on the back of the animal, which has been called uterus, perhaps erroneously, and there undergo development. But at certain seasons many of these Entomostraca produce ova of a different kind from those now referred to. To these the name of winter or hybernating ova has been given, as they appear to be adapted, from the strength and impermeability of their external coverings, to resist the injurious effects of cold and other atmospheric influences during the winter season. These ova are generally in smaller number than those of the ordinary kind, frequently two, sometimes only one; and they are contained and undergo development in a peculiar case, which is formed on the back of the animal below the shell, nearly in the same situation as the matrix for the ordinary ova. This case, which afterwards separates from or is abandoned by the animal, forms a sort of hump or saddle on its back, and has hence been named the ephippium, and the eggs have been called ephippial ova. These ephippial ova, according to Baird, are already fecundated by the original impregnation of the female parent, and do not require, for themselves nor for their progeny for several generations, any renewed or special impregnation.

It appears from the observations of Jurine, Strauss, and Baird, that at the time when the ephippial ova are about to be formed, a sudden change takes place in the appearance of the ova, by the deposit of a quantity of dark granular substance. This appears to be transferred into the cavity behind, in which an increased growth of substance round the ova and within the shell gives rise to the production of a two-valved case for containing the ova. According to S. Fisher of St. Petersburg[*], the formation of the ephippial ova may be noticed during the whole season, from the middle of July onwards; and it may therefore be inferred that these ova have for their object the preservation of the species in the heat of summer when the ponds are liable to be dried up, as well as by resisting the cold of winter.

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* Nat. Hist. of the British Entomostraca, Ray Soc. Public., p. 79.

Von Siebold[†] states that these hybernating ova contain no germinal vesicle; and Dr. Burnett, in his translation of Von Siebold's work, has adduced various arguments in favour of the view that this is an instance of "internal gemmiparity" (as he regards the corresponding phenomenon in Aphides) rather than the production of true ova. Sufficient data are still wanting, however, to form a decided opinion on this subject, as we cannot at present distinguish between the ova of the Entomostraca which are the result of fecundation, and those which are formed and developed independently of the concurrence of the male.[‡]

Annulata.—In the class of Annulate Worms, including the Leeches, Earthworms, Nereids, and Amphitrites[§], although considerable varieties present themselves in the modes of reproduction, there is yet a greater degree of uniformity in the structure of the ova than in some of the classes previously referred to.

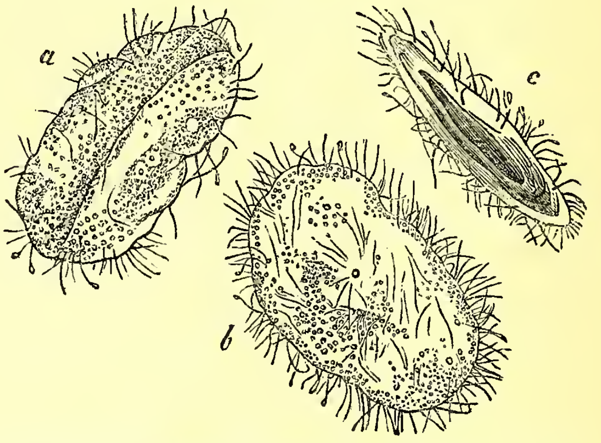
In the greater number the ova are nearly spherical in form, of rather small size; the yolk-substance is generally finely granular, and segmentation is complete; the germinal vesicle is clear, with a distinct single macula, or one which is elongated or only slightly divided into subordinate particles. In most ova of Annulata there is, in addition to the inner transparent vitelline membrane, a chorion or external membrane of considerable strength, and not unfrequently a superadded layer of albuminous substance, which unites the ova in groups or cocoons, or serves to attach them to other bodies.[‖]

In Clepsine, among the Hirudinea, the yolk-substance differs from the common form above described, being composed rather of larger-sized globules; and in another genus belonging to the same order, Piscicola, according to Leydig[¶], there are peculiarities of structure which have not as yet been referred to any general law. In the ova of these animals the covering is double, consisting of a delicate internal vitelline membrane, and an external envelope or chorion, to which a layer of distinct flattened and nucleated cells is adherent; and within the vitelline membrane there is a collection of nucleated cells which displace and partially surround the usual finely granular or formative yolk-substance. Leuckart[*] informs us that the same peculiarity exists in Pontobdella; but the nature and destination of this inner cellular part of the ovum does not appear as yet to be understood in either of the animals mentioned.

In the Piscicola, Leydig observed the ovum, while within the ovarian cavity, to be completely surrounded for a time and enclosed by a consistent mass or covering of spermatozoa; and it has been observed that in this animal the germinal vesicle has not in general disappeared till some time after the ovum has thus encountered and been enveloped by the mass of spermatic substance.

In the Lumbricus, Meissner[†] has made the novel and interesting observation, that previous to the encounter of the spermatozoa with the ovum, the latter loses the vitelline membrane which before covered it, and that the spermatozoa then penetrate, in great numbers, the whole surface of the exposed yolk.

Fig. 82*.



Ova of the Lumbricus during fecundation. (From Meissner.)

The figures represent three views of the ova of Lumbricus agricola, *a.* & *b.* on their flat sides, *c.* seen edgeways. Over the surface spermatozoa are seen penetrating the vitelline substance, giving to it on a large scale the appearance of a ciliated surface. The ovum which has now reached the receptaculum seminis is without vitelline membrane, the yolk being thus directly exposed to the action of the spermatic masses; but the vitelline membrane existed at an earlier period and disappeared by solution in the course of the descent of the ovum.

The development of the ova in Hermella has been minutely described by Quatrefages; and this may be taken as an example of the general nature of this process among the

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[*] Mem. of the St. Petersburg Acad., 1848, tom. vi., p. 162.

[†] Compar. Anat.

[‡] See Burnett, loc. cit., p. 353; Zencker, über die Daphnoidæ in Müller's Archiv., 1851, p. 112; and Leydig, über Artemia salina und Branchipus stagnalis, in Zeitsch. für Wissen. Zool., vol. iii. 1851, p. 297.

[§] Suctoria, terricola, errantia, and tubicola.

[‖] For a clear and comprehensive account of the reproduction of the Annelida in general, and with special reference to the genus Hermella, one of the suctorial Annulata, the excellent memoir of Quatrefages, in the Annal. des Scien. Nat., 1848, vol. x. p. 153, in which, in addition to his own researches, are duly recorded those of previous observers.

[¶] Zeitsch. für Wissen. Zool., vol. i. p. 123.

[*] Article Zeugung, p. 809.

[†] On the penetration of spermatozoa, &c., in Zeitsch. für Wissen. Zool. vol. vi.

Annelida. According to this description, the first germs of the ova consist of minute germinal vesicles formed in the ovarian substance; they soon acquire the single macula or nucleus. After undergoing some enlargement, these germs fall into the abdominal cavity, and there acquire, by deposit round them, the clear primitive vitelline substance. In this substance opaque granules, which are at first colourless, are subsequently deposited; and as these extend outwards from the germinal vesicle, and accumulate in quantity so as to increase the bulk of the whole ovum, a delicate vitelline membrane is added externally. The germinal vesicle attains a diameter of about $\frac{1}{950}''$, and its macula of $\frac{1}{2500}''$; and when the several parts of the ovum which have been mentioned have appeared, and the yolk is now coloured, the whole ovum has a diameter of about $\frac{1}{330}''$.

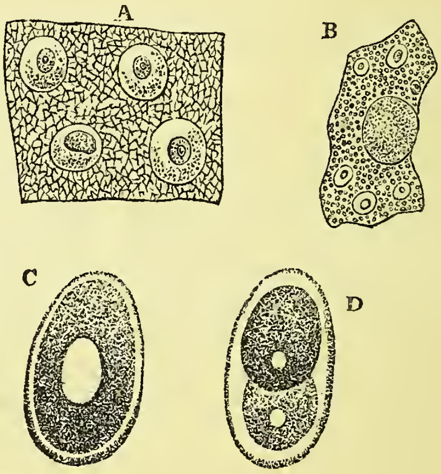
The superficial part of the yolk consists of minute coloured granules. Within this there are larger oil-like globules free of colour, and in the innermost part a somewhat viscous transparent fluid.*

According to Leydig, the germinal vesicle in Piscicola becomes enveloped by a second vesicle or cell-wall before the formation of the yolk-substance; but it is suggested by Leuckart that he may have been misled in this by the appearance often presented by the clear and somewhat highly refracting substance which in many animals precedes the formation of the opaque yolk. If this is not so, the fact observed by Leydig would constitute a marked departure from the usual homological relations of the ovum.†

Rotifera. — Although most zoologists are now disposed, on the ground of the analogies in the most important parts of their general structure, to place the Rotifera among or close to the Articulate Worms, yet in some respects their mode of reproduction presents a marked correspondence with that of the lower Crustacea. Thus they have, in common with some of the lower Crustacea, the occasional separate condition of the sexes, the preponderance of females, the imperfect development of the males, the proportionally large size of the ova, and the production of winter ova as well as the ordinary kind; on the other hand, the simpler structure of the ovum and its complete segmentation are more similar to what is observed among the Vermes.‡

The relation of the sexes in Rotifera has only recently been in any degree understood, and that only in a few genera; and there are still many points requiring elucidation. The greater number of the animals, in fact, which till lately have been known or described in this class have been females; and as yet the males or male organs have been ascertained only in a few genera. Some are certainly of separate sexes, as Notommata, and the allied Rotifer of which the male was first discovered by Brightwell*, and of which the development was described by Dalrymple†. Others seem to be hermaphrodite, as in Megalotrocha, described by Kölliker‡; in Euchlanis, by Schmidt§; and in Lacinularia socialis, by Leydig.|| But according to Huxley¶, there may still be some doubts as to the bodies described as spermatozoa, and as to the arrangement of the male organs in the Lacinularia.

Fig. 83*.



Ovarian ova of Rotifera. (From Huxley.)

The figures represent the formation and development of the true or ovarian ova of Lacinularia socialis (one of the Rotifera). A. and B. are small fragments of the ovarian substance showing the primitive ova with their germinal vesicles and maculæ; in B. one of the ova more advanced than the rest. C. represents the mature ovum. D. the same undergoing the first stage of segmentation.

The ova of Rotifera have been observed by Ehrenberg and many other microscopists. They are of comparatively large size, but yet belong to the group of ova possessing the simpler kind of structure, the yolk substance being quite finely granular, and undergoing a complete segmentation. The germinal vesicle is large, and possesses a distinct single macula; and the whole ovum is inclosed in a clear vitelline membrane. No micropyle has yet been discovered, nor have the time and

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* Quatrefages, it is to be observed, designates the enveloping membrane ovarian and not vitelline membrane, which last he holds is wanting in these ova.

† Farther interesting views of the ova of this class will be found in Milne Edward's memoir in the Annal. des Scien. Nat. for 1845, vol. xxiii. p. 145; and in his article ANNELIDA in this Cyclopædia, to which I must refer the reader; in Grube's Untersuch, über die Entwickel. der Clepsine, Königsberg, 1844. H. Koch, Ein Worte zur Entwick. von Eunice, with an Appendix by Kölliker, on Exogone and Cystonereis.

‡ See Leydig, On the Structure and Systematic Position of the Rotifera, &c., in Zeitsch. für Wissen. Zool., vol. vi.; and C. Vogt on the same subject in vol. vii. of the same work.

* Ann. of Nat. Hist. for Sept. 1848, p. 153.

† Philos. Transact., 1849, p. 331.

‡ Froriep's Neue Notizen, 1843, p. 17.

§ Vergleich. Anat. p. 268.

|| Zeitsch. für Wissen. Zool., vol. iii.

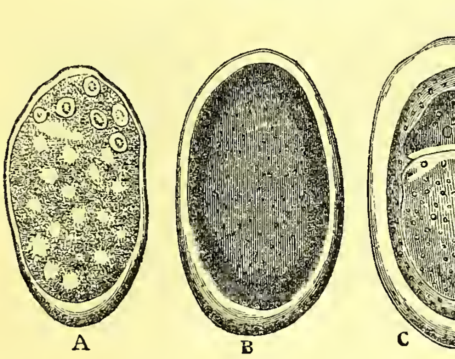
¶ Microscop. Soc. Trans. p. 1. in vol. i. of Microsc. Journal, 1853.

phenomena of fecundation been minutely observed.

The formation of these ova may be traced with facility in the substance of the ovary, in consequence of the transparency of the animals. The nucleated germinal vesicle seems first to make its appearance; the granular yolk substance follows; and the vitelline membrane is last formed.*

The Rotifera present another example of the formation in the autumn season or before winter, of that variety of the reproductive body which has been called winter egg, and which has already been noticed under the Entomostraca. These bodies were observed by Ehrenberg in Hydatina and Brachionus, by Dalrymple in Notommata, and by Huxley and Leydig in Lacinularia. They are twice the size of the ordinary ova, are formed in very small numbers, probably only two, as is most common in Daphnia, and contain no apparent germinal vesicle. Mr. Huxley† appears to have pointed out very clearly the distinction between true or ordinary ova and these reproductive bodies. He says, at p. 16 of his paper, "The true ova are single cells which have undergone a special development, the ephippial ova are aggregations of cells, in fact larger or smaller portions, sometimes the whole of the ovary, which become enveloped in a shell and simulate true ova." Mr. Huxley has traced minutely the process of conversion of the substance of the ovary into such an ephippial ovum, or rather the protecting covering of the two ova which are contained in the ephippium; and his observations seem to show a manifest difference between these and the ordinary ova. The same follows also from Mr. Dalrymple's researches on Notommata. The correspondence of the number and general structure of these ova in Daphnia and the Rotifera is also deserving of notice. These winter ova, besides being much larger than the ordinary ones, differ from them also in structure, having three investing membranes; and they appear designed, like those of the same kind in other animals, to resist the cold of winter and other hurtful influences.

Fig. 84*.



Formation of Ephippial ovum in Lacinularia Socialis. (*From Huxley.*)

A. represents a portion of the ovary massed together and undergoing a change of structure preparatory to its conversion into the ephippial ovum.

B. the ovum now complete, the external investment distinct.

C. the same having now its contents divided into two portions. The ephippial ova differ from the ordinary ones in their mode of formation, and in having three investments.

It would appear that these ephipphial ova, like those of Daphnia, do not require fecundation. Leydig, though distinguishing the two kinds of ova, regards the hybernating ova as only modifications of the ordinary ones; while Huxley considers them rather as peculiar buds like those of Aphis or Gyrodactylus.*

Turbellaria.—Under this class three orders of the animals allied to the Planaria may be brought, according to the researches of Quatrefages and others, viz., the two kinds of Planaria with simple and ramified alimentary canal, or Rhabdocœla and Dendrocœla, and the Nemertides or Miocœla. The first two orders are hermaphrodite; in the third the sexes are distinct. The ovology of this class is known principally from the interesting and beautiful researches of Quatrefages †; but the history of the structure and formation of the ova is still far from being complete.

The ova of the Planariæ are of various magnitudes, and present some differences in their structure. For the most part they contain only the finely granular yolk, but with occasionally some oil globules interspersed. It is only in the earliest stages that the germinal vesicle is perceived with ease, in consequence, probably, of the opacity of the yolk-substance, and the dark colour of the external envelopes.

In most of the genera the germinal vesicles and the yolks are formed in separate organs, as in the trematode animals, to which the Planariæ are nearly allied, but in some, as Macrostomum, these two organs come to be combined in one. At first the yolk-mass, in descending and meeting with the germinal vesicles, unites a number of them into a connected chain; but somewhat later the ova are separated into distinct spheres, and a vitelline membrane is formed to enclose each of them.

Just as occurs in the body of the adult Planariæ, there is also in the ova a remarkable tendency to subdivision by fission. Thus, in the commencement of the development of the ovum, it is liable to become divided into distinct masses, so as to give rise to the development of a number of embryoes from one ovum. Such, at least, is the view entertained by some; but there may be doubts as to whether the ovum so divided is really simple, or is rather a collection or aggregation of a number of germs surrounded by a common yolk; in fact, as has been suggested, an ovarian sac containing a number of ova.*

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* Leuckart, loc. cit.

† Loc. cit.

* See on this subject also, Burnett's translation of Von Siebold's Comparative Anatomy, p. 150.

† Mém. sur quelques Planariées Marines, in Annal. des Scien. Nat. 1845, tom. iv. p. 169; and Mém. sur la Famille des Nemertiens (Nemertea), id. lib. 1846, tom. vi., p. 269. The Rhabdocœla are known chiefly by the researches of Schmidt, Die Rhabdocœlen Strudelwürmer des süssen Wassers, Jena, 1848; and of Schultz, Beiträge zur Geschichte der Turbellarien, 1851.

The manner in which the spermatozoa reach the ova for fecundation does not appear to have been ascertained with accuracy.

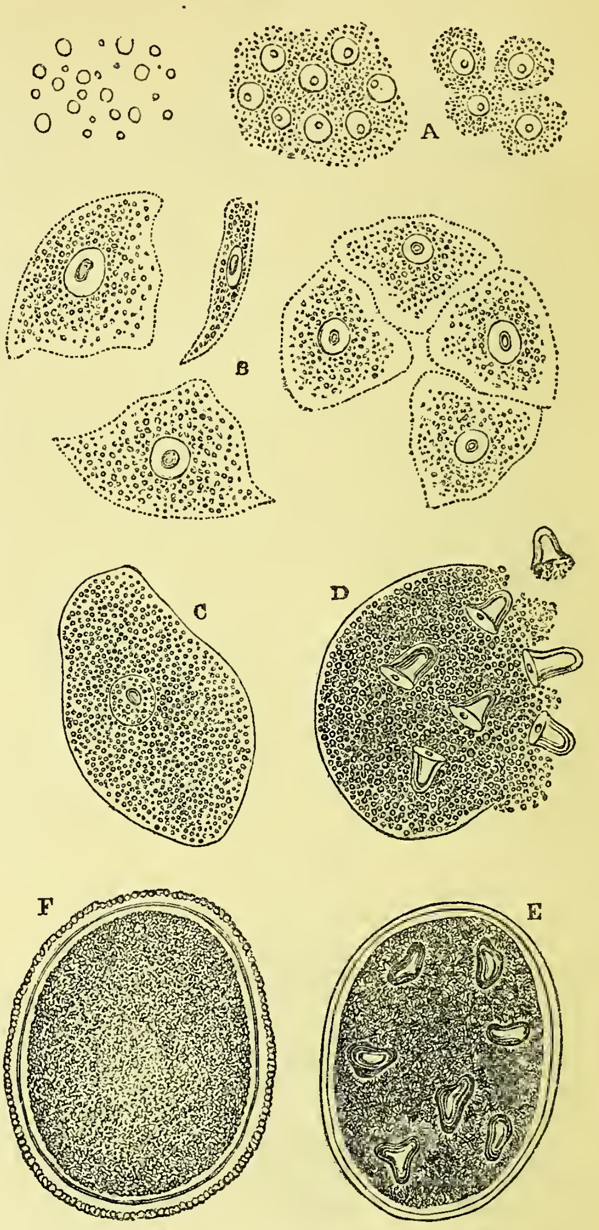
Entozoa.—The ovology of the Helmintha or Entozoa has received considerable attention from physiologists, both on account of the interesting nature of the phenomena presented by its study, and because of the anxiety to discover the mode of production of these parasites within the bodies of other animals. From the researches on this subject which have been prosecuted with great assiduity by a number of observers in recent times, not only have many doubtful points been solved as to the origin of the Entozoa, and the views of naturalists greatly modified in regard to the history of these animals, but considerable assistance has also been received in the elucidation of general questions in ovology. I will give a short sketch of what has been most recently ascertained on this subject under the three divisions of the Nematoidea, including all the Round Worms, the Trematoda, and the Cestoidea including the Cystica. All the animals belonging to the first division are bisexual, and the production of the embryo is direct from the ovum, without metagenesis or metamorphosis; in the two other divisions hermaphroditism prevails, and development is indirect, or accompanied by metagenesis and metamorphosis in the greater number.

Nematoidea.—The genital organs in the first of these orders present the same favourable circumstances as those of Insects for the observation of the structure and formation of the reproductive elements in their successive stages, as in the different parts of these tubular organs there are to be found at once the spermatic cells and spermatozoa, and the germinal cells and ova in every conceivable degree of advancement from their earliest apparition to the state of maturity.

In the Ascarides and most of the round worms, the upper closed extremities of the two genital tubes of the female correspond with an ovary, or rather as a portion of it which may be regarded as a germ-forming organ; for in this upper part of the tube are produced only the nuclei or nucleated cells, from which the germinal vesicles derive their origin. A second portion of the tube, in which the granular yolk substance is added, is to be looked upon also as a constituent part of the ovary, and may be called the yolk-forming or vitelligenous organ. Next follows a constricted part of the tube, which may be termed oviduct, in which the ova meet with the spermatic corpuscles and undergo fecundation. From this the ova pass into the fourth compartment, a dilated portion which has been called a uterus, and below this the two genital tubes finally unite into a common vagina.

In the Ascarides, the process of formation

Fig. 85*.



Development and fecundation of the ova of Ascaris mystax.

A. Earliest stage of the ova as they are found in the cœcal or uppermost part of the ovarian tube; some from the highest part are mere molecules, others a little farther down are minute nucleated cells (germinal vesicles or germs of the ova), and round these the primary yolk granules are beginning to collect.

B. Ova from the second part of the ovarian tube in which they are closely pressed together and arranged in a radiated manner round the axis or centre of the tube. To the right, four of these ova are represented adhering together; to the left, two ova are shown with their flat surfaces, and one with its thin edge towards the observer. The external dotted line represents the surface of the basement substance of the yolk in which the opaque vitelline granules are deposited; there is as yet no vitelline membrane; the germinal vesicle and macula are very distinct.

C. An ovum from the oviduct; a faint marginal line indicates the place where the vitelline membrane is afterwards formed. The germinal vesicle still visible, though obscured by the yolk granules; the ovum has now assumed an ovoid shape.

D. Softened state of the ovum at a slightly later stage, when it has met with the spermatic corpuscles; which are held by Nelson thus to penetrate or gain access to the vitelline substance.

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* Burnett's transl. of Siebold's Compar. Anat. p. 140.

E. Ovum more advanced; the vitelline and albuminous membranes formed; clear highly refracting spaces resembling altered spermatic corpuscles are seen in the yolk substance.

F. Ovum after fecundation; uniform structure of the yolk substance previous to the appearance of the embryonic cell and commencement of segmentation. The chorion has now become tuberculated.

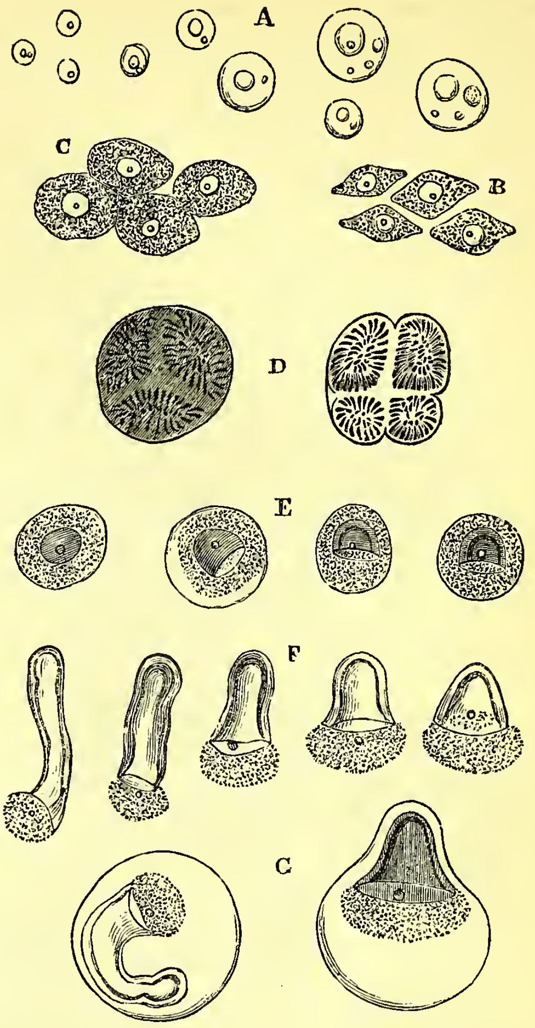
of the ova appears to consist, first, in the production of minute cell-germs in the uppermost part of the ovarian tube immediately adjoining its cœcal termination. It does not appear to be fully ascertained whether these germs are originally, as some have supposed, the maculæ or nuclei, or rather, as others hold, the germinal cells or vesicles themselves: the latter opinion appears to be the most probable. Second, the granules of the yolk-substance very soon collect round the exterior of the germinal vesicles. These granules appear at first to be suspended in fluid; but a little later, as they come to collect round the germinal vesicles, they are united together in a mass by a firmer but clear basement substance, and when the minute ova have somewhat increased in size, the outline of this clearer basement substance of the yolk is distinguishable. There is not, however, at first any external or vitelline membrane; of this Dr. Nelson and I have convinced ourselves by repeated observations in Ascaris mystax.*

The ova, as they continue to descend in the vitelligenous part of the tube in immense numbers closely pressed together, assume the form of subtriangular flattened bodies, and come to be arranged in series of three, four, or more, in a short spiral round the centre of that part of the ovarian tube which constitutes the yolk organ, as round a central axis, but without being united together by any common stalk or other structure. A prodigious number of ova are thus packed together in a very small space.

In passing through the next part of tube, which forms an oviduct, the ova are detached from the spiral and closely-set position, and being surrounded by fluid, which must here be secreted within the tube, descend one by one through its narrower part. At this place they encounter the spermatic corpuscles when they are present, and undergo the change of fecundation; but whether fecundated or not, the ova now lose their germinal vesicles, alter their form from that of flattened triangles to oval, become for a time much more yielding and soft, and somewhat later begin to acquire an external covering which they have not previously possessed.

The peculiar motionless and tailless spermatic corpuscles appear, therefore, to come into contact with the ova when the yolk is exposed directly to their action. According to the interesting observations of Dr. Henry

Fig. 86*.



Development of Spermatic Corpuscles in Ascaris mystax.

This figure is introduced to show the several stages of development of the peculiar acaudal and motionless spermatic corpuscles of the Ascaris mystax.

A. shows various stages of the primary sperm-cells or rather sperm-germs; in the more advanced of which towards the right, internal cells are seen forming by endogenous production within the primary germ-cells.

B. & C. show the second stage, in which the separated germ-cells have each become covered by a finely granular mass collected round them; in B. this process is beginning; in C. it is completed, and the sperm cells thus formed have assumed an ovoid shape.

D. Two views of sperm-cells in the third stage, in which a quadrifid division of the whole cell has taken place preparatory to the escape or separation of the spermatozoon-cells, usually four in number, proceeding from each sperm-cell.

E. Various views of these spermatozoon cells in which the radiated linear marking (seen in D.) has disappeared, and is again resolved into granules; the nucleus is seen from above in the left-hand figure; in the three others being viewed in profile the appearance of the bell-shaped spermatic corpuscle with the nucleolus is perceptible.

F. Exhibits from right to left the various progressive stages of the bell-shaped corpuscle into the test tube form; the remains of the nucleolus and granular substance are seen towards the mouth of the flask-shaped bodies.

G. Illustrates the effect of water in developing "Sarcode" on the exterior of these corpuscles in two different stages of their advancement.

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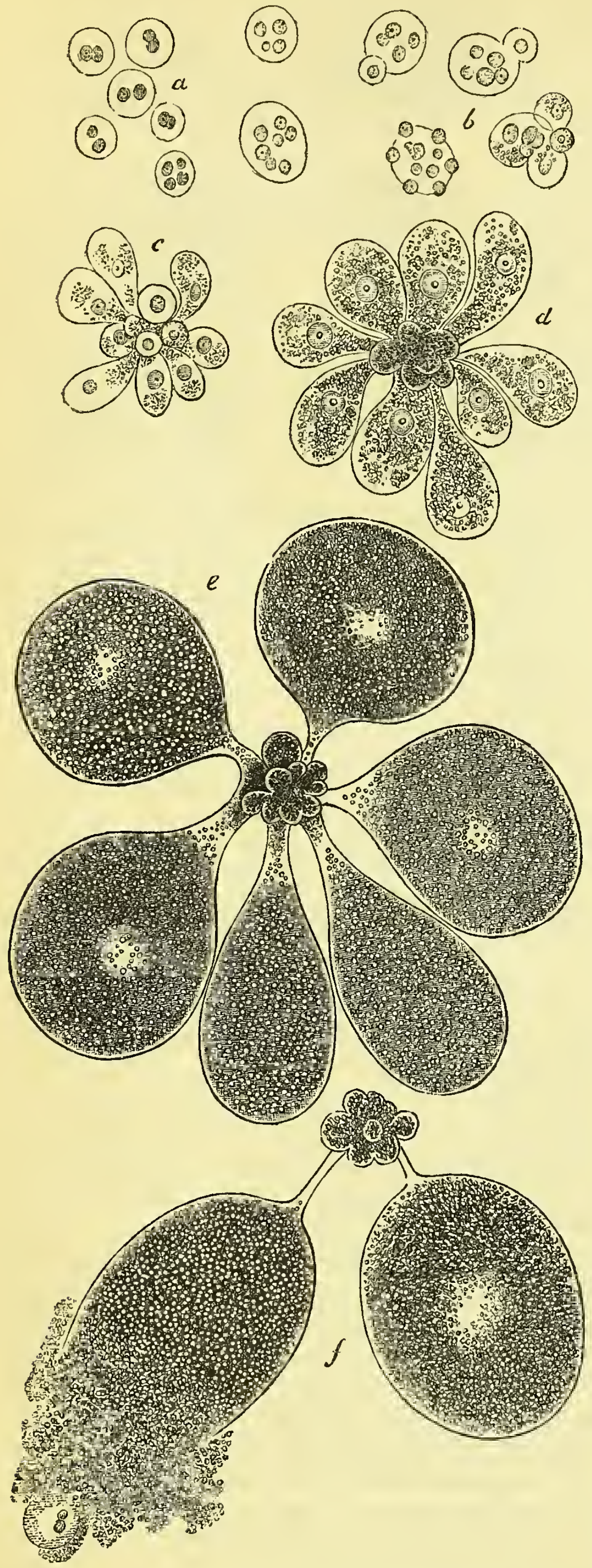
* See Nelson's paper on the Reproduction of the Ascaris Mystax in the Trans. Roy Soc. of Lond. 1852, p. 563., pl. 28, figs. 48. and 50.

Nelson,* a peculiar softening of the ova, which may be caused by the rapid imbibition of fluid at the time the changes above mentioned are taking place, renders them peculiarly liable to be impressed by the spermatic corpuscles at this period; and Nelson is of opinion that these corpuscles even penetrate completely into the yolk-substance, and ultimately combine with it. Little doubt can be entertained that a combination of the spermatic and vitelline elements in some manner takes place at this time, whether by the direct interpenetration after the mode described by Nelson, some may be inclined to doubt; but at all events the spermatozoa act immediately on the vitelline substance at this stage of the progress of the ovum. *

As the ovum descends in the next part of the tube or uterus, the external membrane becomes more dense, additional layers are deposited upon it, and at last it acquires more

Fig. 87*.



Development of ova in Mermis albicans, belonging to the Gordiacei. (*From Meissner.*)

a. Germ-cells from the upper or cœcal end of the ovarian tube, their nuclei undergoing subdivision.

b. Various stages of farther multiplication of the internal cells, which in the more advanced are seen to approach the surface of the original cell, and to cause the bulging of its membrane by the enlargement of the internal cells, which last constitute the primitive ova.

c. & d. Groups of primitive ova thus formed; some of them much more developed than others, presenting internally the nucleated germinal vesicles and yolk granules and attached in pediculated capsules, which are formed by the extension of the membrane of the primary germ cells.

e. A group of these ova more advanced; the opaque granular yolk increased in quantity so as to obscure in part the germinal vesicles; the pedicles much narrowed and somewhat elongated; the external ova are nearly mature; those in the centre remain abortive.

f. Two similar ova now ripe, a part of one of them is artificially burst, showing the escape of the yolk granules and germinal vesicle with a double macula. The remains of the pedicles when detached from the central mass constitute, according to Meissner, the micropyle aperture.

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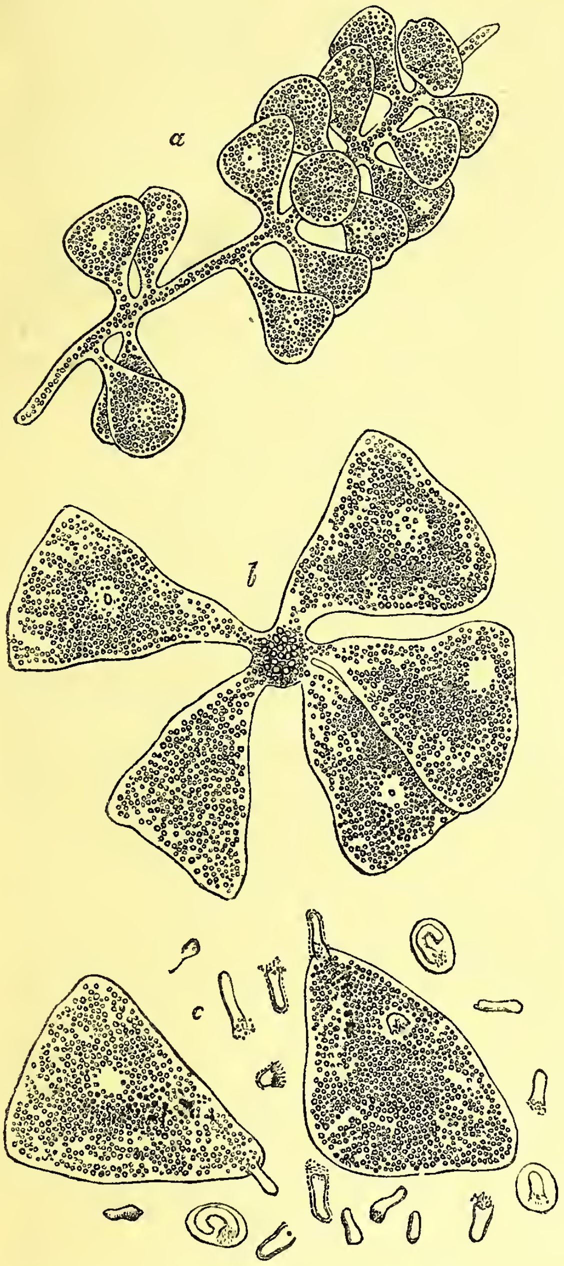
* Loc. cit., p. 576.

* Professor Bischoff has, in his recently published tract "Wiederlegung des von Dr. Keber bei den Naiaden und Dr. Nelson bei den Ascariden behaupteten Eindringens der Spermatozoiden in das Ei," &c., Giessen, 4to., 1854, called in question the accuracy of Nelson's observations, and asserted that Nelson's spermatozoa are only epithelial particles belonging to the female passages. In a subsequently published paper, entitled, "Bestätigung des von Dr. Newport bei den Batrachiern und Dr. Barry bei den Kaninchen behaupteten Eindringens der Spermatozoiden in das Ei, Giessen, 25th March, 1854," although Bischoff has seen reason to alter his previous views as to the phenomena of fecundation in the Ascaris mystax, he still in that paper, and in a special memoir on the subject, published in the Zeitsch. für Wissensch. Zool., 1854, vol. vi. p. 377. adheres to the view that the bodies which I, along with Nelson and Meissner, regard as spermatozoa are no more than epithelial cells. I have elsewhere shown that this view is altogether untenable, and that no doubt can now prevail as to the corpuscles in question being the product of development from the spermatic cells of the male Ascaris, and as to the possibility of their direct action on the ova within the female previous to the formation of the vitelline membrane. Meissner has also given the most satisfactory evidence on the same point in his memoir on the penetration of the spermatozoa into the ova of animals, contained in the same volume of the last quoted work, though this author takes a different view from Nelson and myself as to the manner in which the spermatozoa are admitted into the ovum in Ascaris mystax, believing in the existence of a vitelline membrane and micropyle, in the same manner as in Mermis and other Gordiacei, which he has so well described. With regard to this view as applied to the Ascaris mystax, Bischoff's observations, Nelson's, and my own, give me the greatest confidence in asserting that there is at first no vitelline membrane in this animal at the time when the ova first meet with the spermatic corpuscles.

or less of a minutely tuberculated structure on its external surface. The ovum becomes of a regular short oval or nearly spherical form. If fecundation shall have occurred, the embryonic vesicle or cell makes its appearance, and the phenomena of segmentation follow in rapid succession.

Fig. 88*.



Formation and fecundation of the ova of Nematoid Worms. (According to Meissner.)

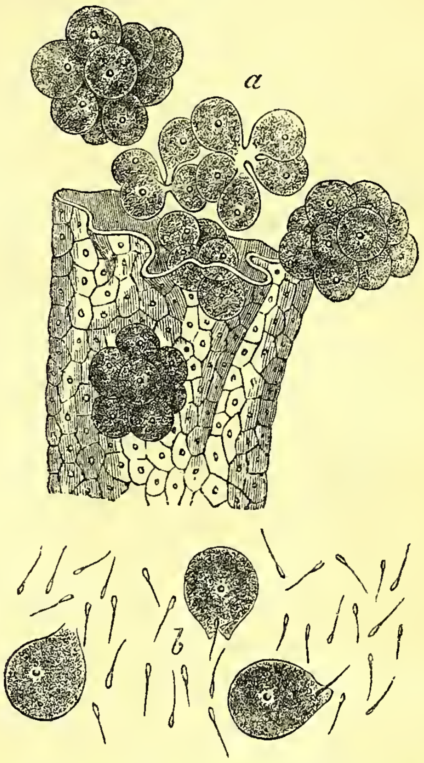
a. A portion of the ovarian axis and early ova attached to it from the ovarian tube of Strongylus armatus. The axis column occupies the centre of the tube, and the ova are suspended to it by pedicles, supposed by Meissner to form micropyle apertures when they are detached.

b. View given by Meissner of a set of the nearly ripe ova of Ascaris mystax, which he conceives are thus connected by pedicles to a central axis.

c. Two mature ova of the same surrounded and in part penetrated by spermatic corpuscles. At the narrow angles of these ova a spermatozoon is seen passing into the interior by what Meissner has regarded as a micropyle formed by the detached pedicle. In the ovum to the right a spermatic corpuscle is seen in the vitelline substance. The existence of such a micropyle aperture and pediculated attachment of the ova in the Ascarides I regard as doubtful.

In others of the Nematoid Worms and more especially in Strongylus and the Gordiacei, it would appear from the researches of Meissner, that the first germs of ova which take origin in the uppermost part of the ovarian tube multiply by an endogenous production, and that in this manner groups or bunches of the primitive ova are produced which are connected together by pedicles arising from the elongated membrane of the original germ-cell which remains as a covering of the whole. A certain number of these ova make progress in development while others probably become abortive. As the ova enlarge they are more spread out in the tube and take something of the spiral disposition which exists in the Ascarides, but with this difference, as already noted, that the various ova remain connected together by the attachment of their pedicles to a central axis or stem running down the middle of the ovarian tube. On the subsequent detachment of the ova by the breaking of these pedicles, according to Meissner, a micropyle aperture is formed in each ovum for the admission of the spermatozoa. The accompanying drawings from Meissner's Memoir will give a sufficiently clear idea of his views on this subject.

Fig. 89*.



Formation of ova and fecundation in Gordius Subbifurcus. (From Meissner.)

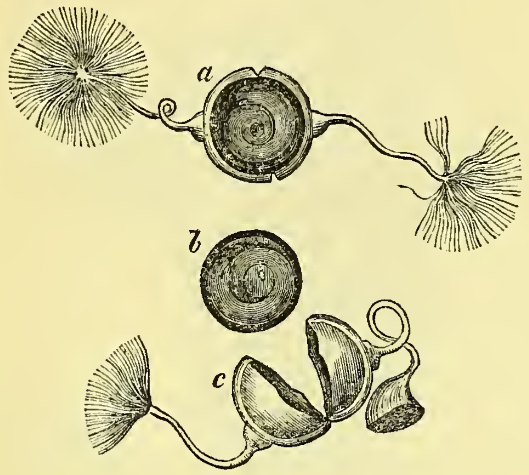
a. A small portion of the ovarian tube with groups of the ova partly within and partly escaping from it.

b. Three of the mature ova from the lower part of the oviduct surrounded by the spermatozoa. The ova are now isolated, and the pedicle of each is open, and is regarded by Meissner as a micropyle, by which spermatozoa, as represented in two of them, enter the ova. The germinal vesicle is still to be seen.

The ova of the nematoid worms constitute a marked example of the simpler kind of ovum in which the formative yolk is present, and in most but not in all of which segmentation is complete. This process was first made known through the interesting researches of Kölliker*, in Müller's Archiv., 1843, p. 68, and Bagge, in his Inaugural Dissertation.† The memoir of Reichert in Müller's Archiv., 1847, contains very correct views as to the formation of the spermatic cells.

The accompanying figure from Meissner‡, gives a representation of a remarkable form of the external capsule of the ova occurring in some of the Gordiacei (Mermis nigrescens).

Fig. 90*.



Mature ova of Mermis nigrescens. (*From Meissner.*)

This figure is introduced to show the very peculiar capsule in which the ovum is enclosed.

a. Ovum taken from the uterus with embryo enclosed; the chorion and shell capsule with chalazæ or brush-like processes attached to the latter.

b, *c*. The shell capsule *c* burst across the equatorial groove, allows the ovum *b* to escape with the chorion and embryo contained within it.

The ova of Trematoda are generally of a long-oval form, and of middle size. They are enveloped by a shell membrane of considerable firmness, and which is not unfrequently of a dark brown colour. The yolk-substance contains fat corpuscles simple and compound; and there is a germinal vesicle present, which, however, from the deep colouration and other circumstances, is often very difficult of detection.

In these animals an interesting peculiarity in the arrangement of the reproductive organs exists, in the separation of the germ-forming and yolk-forming portions from each other; in the first of these organs germinal vesicles or clear nucleated cells alone being produced, in the other the opaque granular fatty matter which furnishes the vitellus. This arrangement was first described by Von Siebold in 1836.§ The germ organ is generally in the form of a rounded sac, which is filled with the nucleated germ-cells or vesicles in various stages of development. The vitelline organ is double, each one consisting of cœcal tubes, in which the opaque granular yolk-substance is secreted.* The ducts of these two organs meet in a common cavity or uterus, and the germs descending into this cavity are there enveloped by a portion of the vitelline mass, and shortly afterwards an enclosing vitelline membrane is formed. These animals being hermaphrodite, the vas deferens of the male organ or testicle leads into the uterine cavity; and it would appear, therefore, that in many cases, if not in all, impregnation takes place by the access of the spermatic corpuscles to the elements of the yolk and germinal vesicle, just at the time when they are brought together to form the ovum.

This separation of the germ-forming and yolk-forming parts of the ovarian organ, which is so apparent in the Trematoda, is not in truth so great a departure from the more familiar structure of other animals as might at first be thought; for, as Leuckart has well observed, there are other examples of the same disposition, or an approach to it. Thus in Insects and in Nematoid Worms, as we have seen, it is from distinct parts of the genital tube that the germs and yolk are produced; and more or less of the same arrangement exists in all instances in which the form of the ovary is tubular.

The Cestoidea present a great similarity to the Trematoda in the arrangement of the organs by which the ovum is formed. Indeed, notwithstanding the difference of their antecedent stages of development, the structure of the mature sexual joint or proglottis of the tapeworm, offers so great a resemblance to that of some of the Trematoda, that they have been regarded as identical by several recent observers. In each sexual joint of the tapeworm, the testicle and the two parts of the ovarian organ coexist, and, as stated in an earlier part of this article, arrive at maturity simultaneously in the posterior or oldest segments of the body. Van Beneden has, in his recent work on the Cestoid Worms†, described very clearly the structure and relations of the germigenous and vitelligenous parts of the reproductive organs in the complete segments or proglottides of a variety of Cestoid worms. The ova originate in the first mentioned of these organs as germinal vesicles, and, passing into the vitelligenous part, meet with the yolk-masses formed there. Near the same place is situated the seminal vesicle, from which, doubtless, the spermatic substance easily reaches the ovum as it descends in the course of its formation. The ova then acquire an external envelope, and pass into the cavity termed a uterus. As they come to be accumulated in gradually increasing quantity in the latter cavity, they distend it to a great degree, so as to cause it to pervade in various forms, ramified and others, the whole body of the proglottis; and finally they are discharged from this, usually after the separation of the joint from the main tapeworm, by the irregular rupture of the outer wall, or by a genital aperture. Here, then, we have another instance of the combination of the several component elements of the ovum together with the sperm, previous to the enclosure of the whole by a membrane so as to give the form of a complete ovum.

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* See his admirable memoir on the first changes in the fecundated ovum, principally referring to the Entozoa.

† Dissert. inaug. de Evolutione Strongyli auricularis et Ascaridis acuminatæ, Erlangae, 1841.

‡ Zeitsch. für Wissen. Zool. vii. pl. ii.

§ Wiegmann's Archiv., 1836, p. 217, Tafl. vi., and Müller's Archiv. 1836, p. 232, Tafl. x., fig. 1.

* See also Thaer on this subject, in Müller's Archiv., 1850, p. 626.

† Mém. sur les Vers Cestoides. Acad. Roy. de Belgique, tom. xxv. 1850, see plate B.

The ova of most of the Cestoidea, as in the common tapeworms, are of proportionally small size. The external envelope is firm, thick, and nearly homogeneous; sometimes, however, presenting a slight appearance of fine radiated striæ passing through it, which recalls the structure of the thick membrane of the Fish's ovum. The vitelline substance is very finely granular, or almost clear; the germinal vesicle is perceived with difficulty, but is of large size.* In some Cestoids the external envelope is of a brown colour, as in the Trematoda, and in others presents peculiar forms and prolongations from its surface. A delicate vitelline membrane is described within the outer covering by some authors.†

The segmentation of the yolk appears to be complete; but this process has been observed only in a few instances.

Of the ova of the Cystic Entozoa nothing need here be said, seeing that it has already been shown that the several genera of this order, viz., Cysticercus, Cœnurus, and Echinococcus, are only larval and aberrant forms of the Cestoid worms, and being immature animals, never produce ova, excepting through their more advanced stage of cestoid development.

Echinodermata. — The different orders and families of this class are all of distinct sex, so far as is yet known, with the single exception of one of the Holothurida, viz., Synapta (S. Duvernæa), described by Quatrefages‡ as presenting a combination of the testicles and ovaries in one organ, resembling in some measure that which exists in the Gasteropodous Mollusca.

In the females of Echinus, Asterias, and Holothuria, the ova have been studied with care by different observers. In all of them the ova present, when mature, more or less of a deep yellow, orange, or red colour, which belongs to the yolk-substance. This substance is finely granular, and is enclosed, at least in some, as Echinus, by a delicate vitelline membrane; but in others, as Holothuria, there is a considerable deposit of an albuminous layer of a peculiar structure, which, from its adhering closely to the vitelline membrane, obscures the latter envelope, and thus has made its existence doubtful to some observers. This albuminous deposit also exists in Echinus, but is in that animal distinguishable from the vitelline membrane.*

The colour and opacity of the yolk-substance in the mature state of the ovum usually prevent our perceiving the germinal vesicle; but in the earlier stages of formation, when the ovum is of lighter colour or even quite clear and transparent, a germinal vesicle with a single distinct macula is easily perceived. This vesicle has disappeared in the ova which are deposited. The segmentation of the yolk is complete in the Echinodermata: the process has been fully traced by Sars in Asterias†, and by various observers in some other genera.

It was in the ovum of Holothuria tubulosa that Professor Johannes Müller first made the novel and interesting discovery of an aperture leading through the thick external membrane towards the yolk; an observation which has been confirmed by various other physiologists‡, and has been productive of important consequences in its extension to a number of other animals in which such an aperture was not previously suspected to exist. Müller brought this observation before the Berlin Academy, and it was noticed in the printed report of the proceedings in 1851. A more detailed account of his observations on this subject is given by Müller in his Archiv. for 1854 (p. 60.). The very thick covering of the ovum of Holothuria presents an appearance of radiated lines running through it perpendicularly to the surface, which resembles in some degree the marking in the membrane of the Fish's ovum, but is not so distinct, and does not appear, as in it, to be produced by visible tubes or pores passing through the membrane. The canal of the micropyle pierces the whole thickness of the radiated membrane; but Müller conceived that it did not perforate the delicate vitelline membrane placed on its inner surface. Leydig, however, and Leuckart are of opinion that the canal passes completely into the interior of all the egg-coverings, and reaches the surface of the yolk, so that it may convey the spermatozoa to that body. The entrance of the spermatozoa has not, however, as yet been actually observed.

According to Leydig, the thick membrane may consist of several layers united together, such as, internally the vitelline membrane, the thick albuminous part in the middle, and externally the nucleated layer formed by the remains of the ovarian capsule. Leuckart and Leydig have also pointed out the fact that the formation of the canal of the micropyle in the egg of Holothuria proceeds from or is connected with the original attached and pediculated condition of the ovum in the ovary, that it is in fact the remains of the divided pedicle after the ovum is separated from the place of its original formation.

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* See Kölliker in Müller's Archiv. for 1843, p. 92; Tafl. vii., fig. 44.

† Details as to the structure of these ova will be found in the work of Von Siebold in Burdach's Physiologie, vol. ii.; in Dujardin's Hist. Nat. des Helminthes, see pl. ix. and xii.; in Blanchard's memoirs in the Annal. des Scien. Nat. for 1848, p. 321; in Van Beneden's work; and in Kuchenmeister's more recent Handbuch der Parasiten des Menschen, &c., Leipzig, 1855.

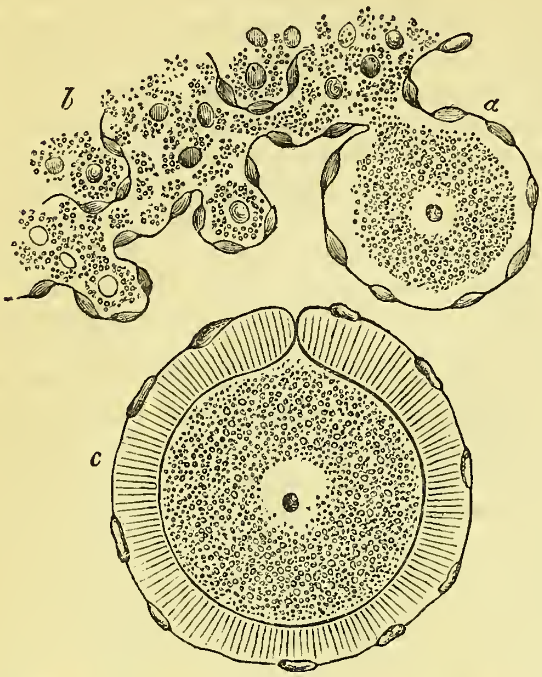
‡ Annal. des Scien. Nat., 1842, xvii.

* Derbès, in Annal. des Scien. Nat. 1847, 3e Sér. vol. viii., p. 80, and Leydig in Müller's Archiv. for 1854, p. 312.

† Wiegmann's Archiv. 1844, and Annal. des Scien. Nat, 3e sér., vol. ii. p. 190.

‡ Leuckart in Bischoff's Wiederlegung, &c., 1854, and Leydig, loc. cit.

Fig. 91*.



Ovum and Micropyle in Holothuria tubulosa. (*From Leydig.*)

a, b. A small portion of the ovary from the inner surface, containing ova in various earlier stages of their development; three of them project from the inner surface, of which *a* is the most developed. In this one the pediculated attachment and enclosure of the ovum by the nucleated ovarian membrane is seen, the yolk granules and the germinal vesicle with its macula.

c. A more advanced ovum now separated from the ovary. Externally the nucleated remains of the ovicapsule are represented; inside this the thick albuminous layer marked with radiated lines, and lined closely by the vitelline membrane; both these, as well as the ovicapsule, being perforated by the micropyle formed at the place where the pedicle formerly existed.

The micropyle aperture has also been observed in other Echinodermata, viz. by J. Müller in Ophiothrix fragilis, in which he states its diameter to be $\frac{1}{1200}''$, and by his son Max Müller in Sternaspis thalassemoides.[*] This aperture has not yet been observed in the ovum of Echinus. In the fecundated ova of this genus, however, Derbès observed spermatozoa to have passed through the thick external albuminous covering, but not within the more delicate vitelline membrane; but in this animal the external covering is more like a layer of soft albumen than a dense membrane as in Holothuria.

The ova of Echinodermata take their origin, like those of other animals, by the formation of the germinal vesicles. These have been observed by Leuckart in the Holothuria tubulosa, beginning to be formed in the ovarian substance, which they cause to bulge or project when they enlarge, so as to hang into the ovarian cavity. The yolk-granules then come to be deposited round the vesicles, rendering the ova opaque, but during all this time the ovum is attached and enveloped by the original capsule derived from the ovary; the albuminous layer is then deposited, and the ovum being detached, the micropyle remains, as already stated, as the perforation in the pedicle of attachment.[*]

Polypina. — Although the greater number of the Polypi are commonly multiplied by a process of gemmation, as has already been stated in a former part of this article, yet they are all capable of attaining sexual completeness, and are also reproduced by means of fecundated ova. From the varieties, however, presented by the form both of the gemmules and true ova in different genera of Polypes, considerable difficulty has been experienced in determining the exact circumstances in which the ova are produced, and the distinction between the germs from which true ova and those from which gemmæ are formed. This is more especially the case among the ciliobrachiate Polypes or Bryozoa, which in their general organisation approach very nearly the tunicate Mollusca, but which in their mode of reproduction resemble closely some of the Polypes.

The ova of the common Hydra, already referred to in a previous part of this article, present the character common to the class, of being enveloped by a firm covering or shell membrane, which seems to be formed from modified cells, and which is sometimes beset with rough processes or projecting bristles or barbed spines somewhat like those of the Bryozoa.

In the Tubularidæ and Sertularidæ the ova are formed in ovigerous capsules, which may be regarded as modified individuals or polype-heads of the compound animal formed by gemmation. In some instances these are detached from the parent stem, as in Tubularia indivisa[†]; in other genera they remain attached, and their ova, or the ciliated embryos developed from them, are discharged from the cavities in which they are formed[‡]; but as the phenomena of the production of these ova have been fully described by Professor Rymer Jones in the article POLYPIFERA, it is unnecessary to enter into farther details with regard to the process in this place.

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[*] The micropyle was represented in the ovum of Holothuria tubulosa by R. Wagner in his Icones Zootomicæ, tab. xxxii., fig. 12., before its nature was known. The first discovery of a micropyle in the animal ovum is therefore due to J. Müller. The next observations of a similar nature are those of Leuckart and Keber.

[*] In addition to the memoirs previously quoted, descriptions of the ova of Echinodermata will be found in the following: viz., those of Comatula by J. Müller, in Mem. of the Berlin Academy for 1841; of Asteracanthion, in Wagner's Prodromus, and in the 5th Part of Carus and Otto's Tabulæ Anat. Compar.; those of Echinus by Derbès, loc. cit.; and by Krohn in Beitr. zur Entwick. der Seeigellarven, Heidelberg, 1849, &c.

[†] Sir John Dalzell, Remarkable Animals of Scotland, &c.

[‡] Dumortier and Van Beneden's Researches, in Mem. of the Acad. of Belgium, 1842, tom. xvi.

In Hydractinia rosea, Van Beneden ascertained the existence of the germinal vesicle and nucleus within the ova while still contained in the capsule; and it appears that in all true ova of the Hydrozoa the vitellus, which consists of finely granular substance, undergoes a complete segmentation in the same manner as in other animals in which it presents a similar structure.

In the common fresh-water polype, in which ovigerous capsules, or ova, and spermatic capsules were found coexistent on the same individuals, I observed sometimes the spermatic capsules brought into contact with the surface of the ova by the bending round of the body of the polype at the time when the spermatozoa were being discharged. This took place previous to the formation of the firm external covering; but I could not determine whether fecundation had thus taken place or whether any spermatozoa had penetrated the ovum.

In some of the Hydrozoa, as in the common green polype, the ova are single, while in others as in Hydra fusca, figured by R. Wagner*, there are several ova enclosed in the same capsule.

It is remarkable that, while in some Hydrozoa the ova are developed from animals which retain the polype form in their complete sexual condition, or from modified polype heads, in others, as in Coryne, Fritillaria and Campanularia dichotoma, it is only from a medusoid progeny separated from the polype stock that the true fecundated ova are produced.

In Anthozoa, the most of which, as Actinia, Alcyonium, Veretillum, Gorgonia, and the Corallines are hermaphrodite, the ova consist of finely granular yolk, germinal vesicle and macula, and undergo complete segmentation.

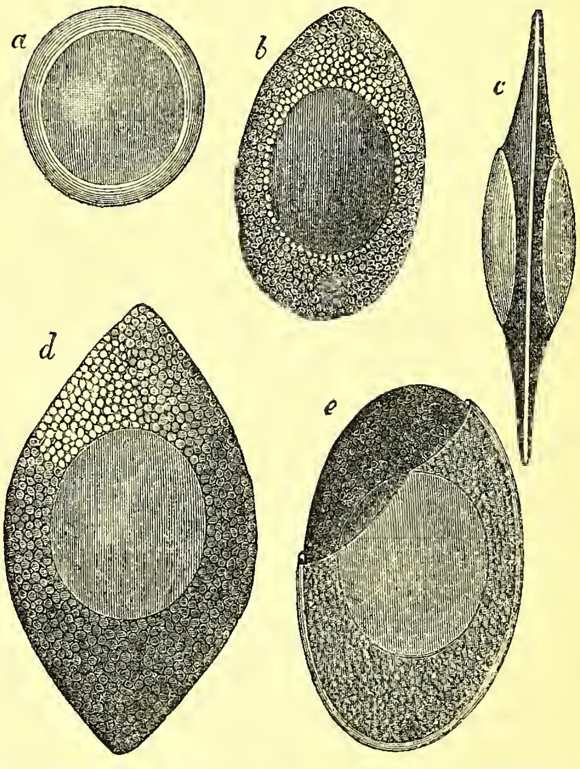
The Bryozoa may be most appropriately considered in this place, as they present considerable analogy to the compound polypes in the mode of their reproduction. They are of separate sexes, and appear to be propagated in three modes, viz.: 1st, by gemmation; 2nd, by true fecundated ova; and 3rdly, by bodies which have long been regarded as ova, but which according to Professor Allman's recent researches may rather be considered as peculiar encysted gemmules, and may probably be analogous to the so-called winter ova of Daphnia and Lacinularia to which reference has previously been made.

The development of the true ova of Pedicellina observed by Van Beneden has been already described.† In this instance the ova are arranged in clusters surrounded by a transparent capsule. In each ovum the finely granular yolk undergoes a complete segmentation. The germinal vesicle possesses a single macula.

According to Van Beneden and Dumortier‡, the ova of Alcyonella are developed in ovarian sacs connected with the inner end of the stomach. They are described as commencing by the formation of germinal vesicles with nuclei or maculæ, and as having subsequently the granular yolk-substance deposited round each vesicle; and these authors describe the same ova as acquiring at a later period the peculiar horny or cellular covering which forms the two-valved shell membrane long known as belonging to the winter ova of this and several other genera of fresh-water polypes. But with regard to the nature of these bodies and the mode of their formation some doubts may arise in consequence of the researches of Professor Allman. The bodies in question are at first nearly spherical and of a light or milky colour; they become later of an oval form, and flattened or discoid, and the cells of the shell-covering are then developed, and acquire the deep brown colour which very generally prevails among these bodies when arrived at maturity, and which makes it impossible to trace farther the changes within the ovum. These cells are developed to a greater extent round the widest margin of the disc, so as to form there a thick ring or border, which is afterwards cleft in two when the valves of the shell open to allow the escape of the embryo.

The same authors have described the propagation of the Paludicella to take place in summer by means of buds, and in winter by

Fig. 92*.



Formation and Structure of the ova of Lophopus Bakeri. (*From Van Beneden.*)

These represent, according to Professor Allman, not the true ova, but the Winter ova or "Statoblasts." *a.* The ovum previous to the deposit of the cellular covering and marginal plate. *b.* This covering now in progress of formation. *c.* and *d.* profile and front view of the ovum, when completed, showing the structure of the cellular border which is afterwards cleft in two at the edge, when the embryo is about to escape.

e. An ovum at an earlier stage showing the ovicapsule in part removed from one side of the ovum and its cellular covering.

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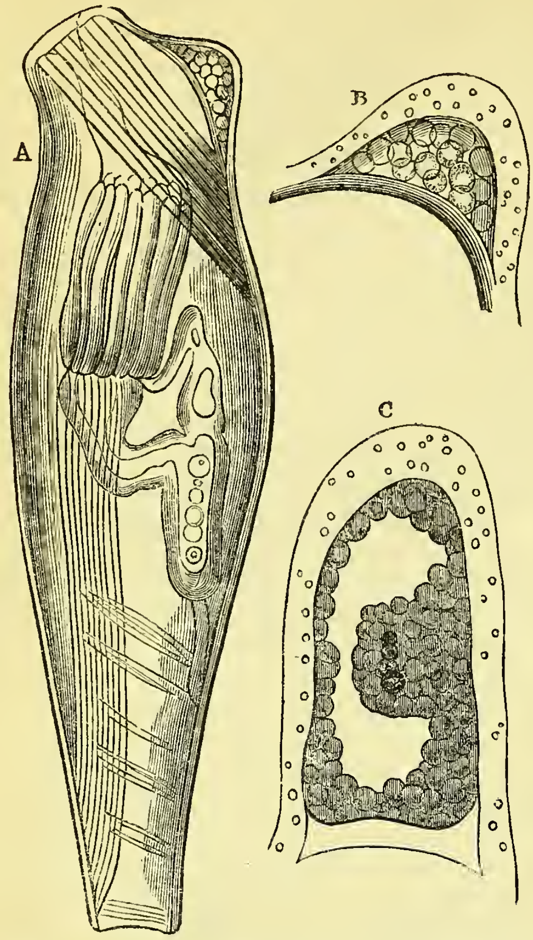
[*] Icones Zootomicæ.

[†] See p. 23. and *fig.* 19. of this article.

[‡] Mém. sur les Polypes d'Eau douce. Acad. de Belgique, 1842.

means of true ova, as well as by attached buds, which last are then covered by a strong corneous envelope, and have received the name of propagula. In Fredericella they describe a propagation by means of buds and by ova provided with the strong horny envelope. In Alcyonella and Lophopus, besides the usual propagation by buds, and by the common ova, these authors have stated that there is also a viviparous production of ciliated embryos from ova which remain within the parent animals; but they have not stated particularly the manner in which these ova originate, nor their difference from those which receive the corneous envelope. The difficulties presented by these varieties seem to be in some measure removed by the view offered by Professor Allman of the nature of the bodies last mentioned, to which I will now advert.

Fig. 93*.



Formation of buds in Paludicella. (*From Van Beneden and Dumortier.*)

a. One of the Polypes of Paludicella Ehrenbergii contracted within its cell, showing at the upper part towards the right the commencement of the formation of the bud by the growth of cells between the outer and inner layers of the cell-wall.

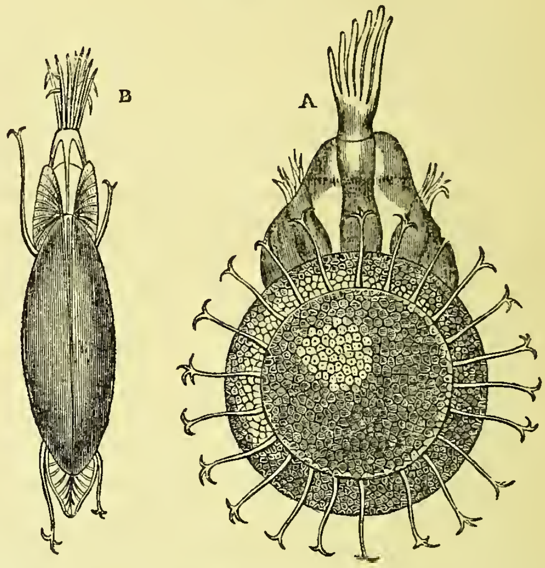
b. The same bud a little more advanced and more highly magnified, represented by itself. The vesicular cells which separate the ectocyst and endocyst are seen more distinctly.

c. A more advanced stage of the same, internally; the part from which the embryo polyped arises is seen bulging out from the rest.

This figure has been introduced to show the difference between the process by which a true bud arises and that by which ova are produced.

It has long been known that the so-called winter ova, or the bodies provided with the corneous envelope, are formed chiefly towards the autumn and winter season; and the strength of their covering has generally been regarded as a provision for the protection of the germ from the hurtful influences of the winter season. During two seasons I have observed the production of these bodies from the Plumatella repens; and I have kept them through the winter till the polypes were developed, and issued from them in the ensuing summer.

Fig. 94*.



Winter ovum and embryo of Lophopus Crystallinus. (*From Van Beneden and Dumortier.*)

This is the same as that represented by Turpin under the name of "Cristatella mucedo." In A. the flat surface, and in B, the narrow edge of the ovum, is represented. The two valves of the egg covering have opened superiorly, and the embryo, which already possesses three crowns of tentacles, is seen escaping.

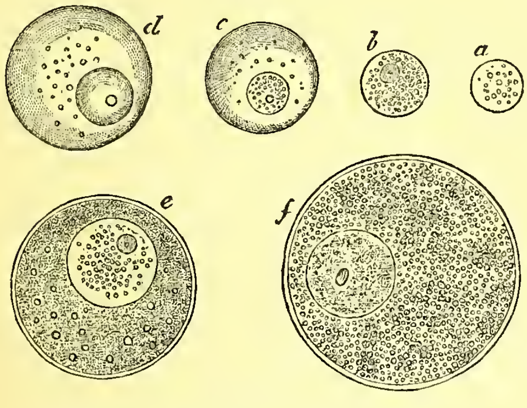
From his careful observation of these bodies in several genera, Professor Allman has arrived at the conclusion that they are not, as was previously supposed, true ova, but rather separated gemmules; and he conceives that Van Beneden, who has described their form and structure so well, must have confounded them with some other bodies in their first or earlier stages, or has failed to distinguish between them and the true ova. This distinction Allman has succeeded in making by ascertaining that the true ova and these bodies do not arise in the same situation, and that these winter ova or gemmules do not in their earliest stages present any germinal vesicle or macula as the true ova do, and do not afterwards undergo any segmentation. They are formed, according to Allman, in the funiculus which connects the bottom of the stomach with the inside of the cell of the polypide, the same body which was described by Van Beneden and Dumortier as an ovary, but which Allman regards rather as analogous to the gemmiferous stolon of the solitary Salpæ. These bodies Professor Allman proposes to call stato-blasts. He farther discovered that there is a true ovary with genuine ova which may be distinctly observed in Alcyonella, and which is situated in the walls of the endocyst near the anterior extremity of the cell. A number of ova were found in the ovary containing the distinct germinal vesicle with macula. He also observed the segmentation of these ova in the usual manner, and the conversion of the segmented mass into a ciliated embryo, within which the new polype is subsequently developed.†

Should these observations prove correct and be applicable to the other instances of similar winter ova among the Bryozoa, they may tend to remove some of the difficulties which exist in regard to the various reproductive bodies occurring in these animals; but farther researches seem still necessary to point out in these and in other polypine animals more fully and minutely the relation between the three kinds of reproductive bodies, viz., true ova, separated gemmules, and attached buds.

Acalephæ.—It is remarkable that notwithstanding the very close relation in which these animals stand to the Anthozoid Polypes, the form of their ova is not the same. The Discophora (Medusæ) are of distinct sexes: the Ctenophora (Beroes) are hermaphrodite; the Siphonophora (Diphyidæ) are various, or bear, in the manner of compound animal stocks, a variety of zoids, sometimes of one sex alone, at other times of different sexes on the same stem.

The structure of the ova in Medusæ is extremely simple. They are originally formed from minute cytoblasts which soon acquire a single nucleus or macula, and are enclosed in a delicate external membrane. These constitute the germinal vesicles, round which the granular yolk-substance is gradually deposited in increasing quantity. The complete segmentation of the yolk has been observed by Von Siebold in Cyanea aurita.* The yolk-substance is often highly coloured, violet or yellow. In the former part of this article I have referred to the manner in which some compound Hydroida are propagated through their medusoid progeny. These medusoid individuals, like the ordinary Medusæ, are of separate sex; and they must therefore be looked upon as the complete stage of the polypine animals from which they have proceeded, whether they have their young developed while the parent remains attached to the nursing polype stock, or have assumed the separate and independent mode of life in a more complete state of development. There are many varieties in the degree of perfection to which they attain even while remaining attached to the polype; but the general principle of formation is the same throughout the whole of the hydroid animals, the remarkable and constant fact with regard to the mode of their reproduction being this, that the immediate product of development from the ovum which has been formed by sexual generation from a Medusa or medusoid animal is invariably an attached Polype, and that the medusa or medusoid is the product of a non-sexual process of gemmation from this polype stem.

Fig. 95*.



Development of the ova of Acalepha.

These figures give magnified views of the different stages of formation of the ova taken from the ovary of a large Rhizostoma. *a.* The primitive germ. *b.* The germinal vesicle now present in the primitive ovum. *c. d.* The same more advanced and enlarged, the macula has appeared in the germinal vesicle, and a few yolk granules are deposited in the clear vitelline substance. *e.* The yolk granules greatly increased in quantity and becoming opaque, a vitelline membrane is now formed. *f.* The same somewhat more advanced, the yolk granules are now collecting together to form corpuscles. The macula is assuming the elongated form.

Protozoa.—With regard to the Protozoa, or Infusoria and Rhizopoda, it is unnecessary to add anything here to what has been stated in the several articles on these subjects and in a former part of this one, excepting the remark, that continued researches appear to show that as the sexual distinction has not been detected, and may probably be absent in these animals, the nucleus of the monocellular forms of these beings may hold the place of the germinal vesicle in them, and that the processes of division and production of internal gemmules takes the place of true ovulation. At the same time it must be admitted that it is by no means improbable that the sexual relations may yet be discovered in the lowest monocellular animal bodies, as has recently been the case in some of the simpler and monocellular Algæ, and that as our knowledge of the process of reproduction in these beings is still very limited, it may be destined to undergo even greater progressive changes than those which it has suffered from the researches of the last few years.†

Porifera.—The bodies which have usually been regarded as the ova of Sponges, and to which a reference was made in the earlier part of this article, are of two kinds, viz. gemmules or detached ciliated portions of the substance of the sponge, and certain spherical bodies enclosed by dense capsules, which are produced towards winter, and which appear to contain a number of germs, each of which is capable of being developed into a Protean animalcule, from which probably a sponge may proceed.* But it may be doubted whether these last-mentioned capsules are true ova or may not rather be of the nature of the gemmules, winter ova, or statoblasts of Professor Allman; and it is important to notice that Mr. Huxley has recently discovered in Tethya a different set of bodies, which contain all the essential parts of true ova, viz. vitelline membrane, yolk, germinal vesicle, and macula, and that these bodies, which are situated between the cortical and central substance, are imbedded in a mass of cells together with spermatozoa.† Although the individual living particles of the sponge closely resemble simple ciliated infusoria, and the mass may, therefore, be viewed as an aggregate of these minute beings, yet its analogies with and transitions towards the fungiform polypes are so great, that we may expect ere long that the phenomena of its reproduction may be placed in a new and clearer aspect by the continuation of the researches now noticed, and by others of a similar kind.

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† Proceedings of British Association for 1855. See also Professor Allman's interesting Report on the Polyzoa to the British Association. See Trans. for 1850, p. 320.

* Beitr. zur Naturgesch. der Wirbellos. Thiere, 1839.

† See the papers of Focke, Cohn, and Stein referred to in the first part of this article, and the more recent work of Stein, "Die Infusionsthiere auf ihre Entwickelungsgeschichte untersucht." 4to. Leipzig, 1854.

RECAPITULATION AND CONCLUSION.

Having now stated in detail the principal facts that have come under our knowledge with regard to the form, structure, and mode of origin of the ova of different animals, it may be proper, in bringing this article to a close, to endeavour shortly to deduce from these facts the most general results to which they appear to lead. These results, together with some reflections on our subject, may be stated under the following heads, viz. 1. Definition of the ovum, as related to its own structure, and its history in connection with the reproduction of the species. 2. Recapitulation of the most general facts ascertained by the comparison of the ova of different animals. 3. Morphology of the ovum; homology of its parts; and relation of the ovum to other organic structures. 4. Phenomena attendant on the maturation of the ovum. 5. Relation of the ovum to fecundation by the male sperm. 6. Immediate effects of fecundation on the ovum; and relation of the ovum after fecundation to the first commencement of the process of embryonic development.

1. Definition of the ovum, as related to its own structure, and its history in connection with the reproduction of the species.

In the commencement of this article the ovum was shortly defined as "the product of parental sexual generation from which the young of animals are developed (produced)." This definition appears correct and sufficiently comprehensive; but should it appear desirable to substitute for it a more precise description of the characteristics of the animal ovum, the following may be proposed as applicable to the ovum throughout the whole animal kingdom, without involving any merely theoretical view of its structure and constitution, viz. "the ovum may be shortly described as a detached spheroidal mass of organised substance, of variable size, enclosed by a vesicular membrane, and containing in the earlier periods of its existence an internal cell or nucleus; these parts, formed by the female individual or organ of animals, are capable, when fecundated by the male sperm of the same species, of giving rise, by the series of histogenetic and organogenetic changes known under the general term of development, to an embryo, from which either directly or mediately the individuals of the animal species to which the parents belong are reproduced."

We thus separate from the category of true ova all those bodies of an apparently reproductive kind which are not the direct product of an act of sexual generation. To such bodies, the nature of which is as yet doubtful, and probably somewhat various, the indefinite appellations of buds, bud-germs, gemmæ, spores, winter ova, ephippial ova, statoblasts, &c., have been given according to the circumstances in which they are severally produced.

In all animals, then, with the exception of the Polygastric Infusoria and Rhizopoda, the occurrence of sexual generation and the formation of true ova are proved to be the regular and constant means for the permanent reproduction or maintenance of the species. In the exceptional instances now mentioned, and even in some others possessed of the sexual distinction, the best known and most common multiplication of individuals takes place by a subdivision of the parent body, either by fissiparous cleaving or by gemmation; but in them also it can scarcely be doubted that there are other means by which the permanence of the species is maintained.

All the most accurate recent investigations lead to the conclusion that the production of the young of all organised beings, even the simplest of the Protozoa, does only occur by direct connection through some organised medium with other beings of a similar kind or species. We are forced, therefore, to conclude that in the propagation or production of these simple beings, in circumstances where their more ordinary fissiparous or gemmiparous mode of multiplication cannot be admitted to have taken place, there must have passed from the bodies of the progenitors minute particles of organised substance (capable, as we know, of being suspended in the atmosphere, and of resisting during a long period many of those influences which generally prove inimical to animal development), which particles, when brought into circumstances favourable to the progress of the vital processes, undergo the cycle of changes necessary for the reproduction of beings similar to those from which they sprang. If there is any constant law which seems more certainly than others to result from all recent researches into the history of organic nature, it is this necessary connection by descent of one being or set of beings from another.

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* See Carter in Annals of Nat. Hist. vol. iv. p. 89.

† See Mr. Huxley's paper in Annals of Nat. Hist., 2nd series, vol. vii. p. 370.

In all animals, with the exception of the simplest tribes already referred to, the descent from parent to offspring is through a product formed and perfected only by the concurrence of male and female organs; but we are still at a loss to determine whether the unseen germinal bodies by which the Protozoa are reproduced are of the same or of a different nature. The structure of some of these germinal bodies as described in the earlier part of this article (p. 7., &c.), bears a very great resemblance to that of true ova; but yet the sexual distinction of the parent animals has not yet been discovered. The recent researches of naturalists indeed show that our whole knowledge of the history of the Protozoa may be considered as only in its infancy. The discoveries as to the encysted stage of existence among the Vorticellæ and Gregarinæ and others, the phenomena of conjugation observed in Gregarina and Actinophrys, the entire knowledge lately gained of the form, structure, and habits of the Foraminifera, all point to important future discoveries and modifications of our hitherto crude and imperfect views of these tribes of beings, and must make us refrain from attempting at present to form any opinion or even conjecture as to the modes of their reproduction; while at the same time the recent discoveries as to the existence of the sexual distinction in the simplest forms of plants encourage the hope that ere long the reproduction of the Protozoa may, in a similar manner, be removed from the obscurity in which it now lies hidden. It does not appear necessary from these considerations that our definition should make any direct reference to animal bodies of the nature of which our knowledge is still so imperfect.

The result of development from a fecundated ovum in all vertebrate and in a considerable number of invertebrate animals, is the formation of an embryo which, by a process of progressive growth, arrives at maturity, and assumes the form, structure, and habits, either, as the case may be, of a hermaphrodite animal, or of the parent of either sex. In a certain number of these instances, as in Batrachia, Insects, Crustacea, and others, growth is not altogether continuously progressive, but is subject to one or more breaks or changes as it were, which are marked by some change in the mode of life, or some difference in structure of the individual. To such marked changes in the course of the development or growth of an individual animal proceeding from a fecundated ovum, the name of Metamorphosis is given.

But from the facts narrated in the earlier part of this article, it appears that in a certain number of the invertebrate animals, such as those which have been referred to under the heads of Echinodermata, Polypina, Acalepha, Tunicate Mollusca, Trematode and Cestoid Entozoa, Annelida and Insecta, a very different result may, either regularly and constantly in some, or only occasionally in others, attend the first development from the fecundated ovum. To this modification of the developing and reproductive process the appellations of Alternate Generation or Metagenesis have been given, of which terms the latter may perhaps be the most appropriate. The phenomena which have been described under this head are so very various, that it is difficult, if not impossible, to give a short and general statement of their nature. The difference between this and the better known form of direct generation may, however, be stated nearly as follows:—In the Metagenetic form of reproduction the individual formed by the development of the fecundated ovum is generally different in aspect, structure, and mode of life from the parent or parents by which the ova were produced; this individual, or zoïd, though possessed, in many instances, of an organisation and of powers which fit it for the efficient performance of many of the most important acts of independent animal existence, is yet wanting in the attribute of perfect animal maturity, viz., the sexual organs and activity, and is consequently incapable by itself of an act of true generation, or, in other words, of the formation of fecundated ova, by which alone the species can be permanently reproduced. In such instances, then, it is only by the formation from these intermediate beings of others which are sexually perfect, that the generative act can be repeated. There are two phenomena requiring to be distinguished in connection with the most common forms of this process; the one the frequent multiplication of the imperfect intermediate beings, or zoïds; and the other the production either directly or by a succession of acts of development from the intermediate beings of those which are sexually perfect, or which resume the form belonging to the parents from which the fecundated ova were derived. It seems proper, therefore, to distinguish between an act of true sexual generation, and that by which new beings are formed from the intermediate individuals (or so-called nurses of Steenstrup, or zoïds of other authors); the first consisting invariably in development from a fecundated ovum; the second being probably more analogous to a process of budding or gemmation from a parent stock. It must be confessed, however, that we have still much to learn regarding the phenomena of this process, before we can form any general notion of its nature. The whole subject is replete with the deepest interest not only in connection with the history of reproduction, but in its influence, as stated in some parts of the preceding article, on the whole range of zoological classification and distinction. Our extended definition comprehends an allusion to these phenomena.

Lastly, the ovum may be considered as having two phases or stages of existence; the one in connection only with the female parent or female organ, in which the greater part of the organised material first to be employed in development is provided, and in which the ovum arrives at a certain stage of maturity; and the other in its relation to fecundation, or to the influence of the product of the male by which its developing powers are awakened or called forth. The mature ovarian ovum may therefore, in one sense, be looked upon as complete, if we regard only its own structure; but here its progress would be arrested without the occurrence of fecundation, and if we view it, therefore, with reference to its more important destination as the means of continuing the animal species, the ovum can only be regarded as perfect when that hitherto inscrutable change has been effected on its substance by admixture with the minute elements of the sperm in fecundation. The constancy of this law in the whole animal kingdom, with the exception of those of the Protozoa already referred to, makes it proper that our definition should make reference to fecundation as the means of perfecting the ovum. To the nature of this process itself a further allusion will hereafter be made.

2. Recapitulation of the most general facts ascertained by the comparison of the ova of different animals.

The ova of animals in their complete state may be considered as consisting of two sets of parts which are of very different relative importance in connection with the development of the embryo: the first of these sets of parts belong to the ovarian ovum, and are formed previous to their quitting that organ; the others are subsequently formed, and may be looked upon as accessory. These last often present great varieties, so as to cause the external form and appearance of the ova of animals to differ widely, while the ovarian part much more nearly corresponds. To this ovarium ovum we shall principally confine our present remarks.

An extended comparison of the ovarian ova of animals belonging to almost every family of the animal kingdom has shown that, notwithstanding great differences in size, and some variation in form and structure, they all agree in consisting of three essential and nearly similar parts before the period of their detachment from the ovary: these are, 1st, The internal nucleated cell or germinal vesicle with its macula or maculæ; 2nd, The vitellus, or yolk-substance; and 3rd, The enclosing vesicular envelope, or vitelline membrane. In all animals there is, also, a general similarity in the manner in which these parts are formed and combined so as to constitute the ovarian ovum; the germinal vesicle is the first produced, and may be regarded as the ovigerm; the yolk-substance next gradually envelopes it or is deposited round the germinal vesicle, and in general the vitelline membrane which encloses the whole is the latest formed.

The most marked differences among the ova of animals are connected with the structure of the yolk and the relation which it bears to the formation of the germinal part out of which the embryo is afterwards developed. Founding upon this difference, three groups, two principal and one subordinate, may be distinguished among the ova of animals:—

1st, The group of small-yolked ova, to which belong those of Mammalia and a considerable number of invertebrate animals, such as most Mollusca, the lower Crustacea, most Annelida, the Entozoa, Rotifera, Echinodermata, Acalepha, and Polypina. In this group, the ovum is generally of small or of moderate size, as a whole; the vitelline substance consists entirely or chiefly of fluid with fine granular particles, and the entire yolk undergoes segmentation: the entire yolk mass, therefore, is directly *formative*, or is employed from the first in the formation of the blastoderm or organised substratum in which the embryo is developed: the germinal vesicle is in this group usually of small size, and has only a single macula, or one composed of very few particles.

The second principal group comprehends the large-yolked ova, such as those of Birds, Scaly Reptiles, Cartilaginous Fishes, and the Cephalopoda, to which, perhaps, may be added Insects, Arachnida, and most Crustacea. In this group, the largely developed yolk contains, suspended in its basement, homogeneous substance, two kinds of organised corpuscles, viz., 1st, A certain portion of the small granular part, similar to that of the small yolked ova, which occupies a limited but determinate place in the ovum, and in its centre the germinal vesicle is situated; and 2nd, A larger portion of spherules, cell-like or other corpuscles of greater magnitude. It is the first or finely granular portion only which is immediately germinal, or which is subject to segmentation and forms the basis of the blastoderm; the remainder, or large cellular portion, is only secondarily employed in supplying nourishment to the embryo or its accompanying organised parts in the progress of their development. In the ova of this group, therefore, we distinguish the formative or directly germinal portion of the yolk-substance from the indirectly *nutritive* portion. In these ova, the germinal vesicle is also proportionally large, and the contents of the vesicle, though consisting in the earliest stages of their formation of a single macula, or of a very small number, very soon become converted into very numerous maculæ, or into a fine granular pulp.

The third, or subordinate group, may comprehend the ova of Amphibia, or scaleless reptiles, and osseous fishes, to which, perhaps, may be added some of the invertebrate animals mentioned under the second group. The ova of this group are intermediate in their structure between those of the first and second: they have certainly the greatest affinity with the large-yolked group, but there are many gradations among the ova of this kind, among allied species of animals, and it is chiefly on the ground of the incompleteness of the segmentation that I have thought it proper to arrange them in a separate group.

It may be remarked further, that in all animals, whatever may be the ultimate structure of the yolk, the primitive yolk, or that which is first formed, is invariably of the finely granular kind, — the cellular or large corpuscular yolk-substance is of later formation. These two parts remain distinct from each other, and the finely granular or formative yolk is that in which the germinal vesicle is invariably imbedded. In those instances, such as the Bird, Reptile, &c., in which the large cellular yolk greatly preponderates over the formative yolk-substance, the latter assumes in the later stages of formation the shape of a flattish disc on one side of the greater mass of the yolk, with the germinal vesicle placed in its centre.

The vitelline membrane presents some varieties in structure, being in some animals very delicate and homogeneous; in others, as Mammalia, remarkably thick, tough, and elastic, but without visible structure; in a third set, exhibiting peculiar structure, such as the finely tubular perforations of the external membrane of the fishes' ovum, or the radiated markings in the ova of Holothuria or Cestoidea; but in these last three instances the vitelline membrane is probably associated with additional layers of substance derived from a different source from that which forms the homogeneous membrane.

A remarkable peculiarity has recently been discovered in the enclosing membrane of the ovarian ovum of some animals, in the aperture or micropyle which has been observed in osseous fishes, insects, some Crustacea*, the Acephalous Mollusca, some Annelida, Holothuria, and some other Echinodermata. There seems reason to believe that a similar aperture exists in the ovum of Batrachia and Cephalopoda; and it is very probable that it may yet be discovered in other animals. At the same time it is right to state that in Mammalia and several other animals it has been most carefully sought for without success. This aperture appears to be designed to admit the spermatozoa into the cavity of the ovum, or into contact with the yolk-substance and germ, in those instances especially in which the egg coverings are thick and tough, and fecundation is late of occurring.

The relation of the ova to the ovaries or organs in which they are produced, exhibits considerable varieties in different animals. 1. The most common is that in which the germs of the ova arise within minute close follicles or vesicles, which are imbedded in the more or less solid or loose stroma of the ovary; the follicle enlarging with the ovum as its other parts are added till the period of of maturity, when, periodically, the follicles open for the escape of the ova. 2. In a second form, as in Nematoid Worms and Insects, the germs of the ova are produced free in the upper part of an ovarian tube, and the yolk-substance, &c. are added gradually as the egg germs descend through successive portions of the tube: here no true dehiscence is necessary to allow of the escape of the ova. 3. In a third form, as in Trematode and Cestoid Entozoa, distinct organs are provided for the formation of the ovigerms and the yolk-substance, and these last are brought together and combined into the spherical form of an ovum in another part of the genital apparatus. 4. In the greater number of animals the germs for each ovum appear to arise singly, and the ova are thus isolated from the first; but it would appear that in some animals these germs arise in groups, perhaps by development from a common germ, so that they are from the earliest period connected together by pedicles. Yet, with all these differences, there is to be perceived, on the whole, a general similarity in the plan of formation of the parts of the ovum itself in different animals. This plan may be generally stated as follows.

The germinal vesicle is universally the first part of the ovum which makes its appearance; it does not appear to be nucleated or to possess its macula from the first in all instances, and this macula cannot therefore be regarded as the centre of its formation. The germinal vesicle is generally at first only a minute point; it soon enlarges, however, and either possesses from the first, or at a very early period acquires, its macula or nucleus. In animals with the solid follicular ovary, each follicle is occupied by a single ovum, which begins within it as a minute germinal vesicle. The delicate wall of the follicle is also perceptible at the same time as the ovigerm; indeed, there is reason to believe that it even precedes the commencement of the formation of the ovum, though this is a point not yet fully determined. In those animals, on the other hand, in which the ovary is tubular, the ovigerms appear, in some instances at least, to arise in groups within cells; and it may be a question whether these cells bear to the ovigerms arising within them the relation of the ovarian follicles of solid or closed ovaries. Whether this be so or not, that relation is in most instances speedily changed, as the ova soon become free, or, in others, are attached by a pedicle to a common stalk.

The wall of the ovarian follicle consists at first of an extremely delicate vesicular membrane, which is the same as that to which the name of ovicapsule or ovisac has been given. At a very early period, and while the ovum consists of no more than the germinal vesicle, the homogeneous wall of the follicle is lined with a layer of flat cells somewhat analogous to some forms of epithelium: this is the commencement of the structure which in Mammalia afterwards forms the tunica granulosa, and the fluid and cellular contents of the Graafian follicle. It appears to have various destinations in different animals.

The second stage in the formation of the ovum is the deposit of the vitelline substance around the germinal vesicle. In most animals the yolk-substance, when it first begins to be formed, is scarcely granular, and in some instances quite clear, consisting of a viscous blastema, and as it increases separating the germinal vesicle within from the ovarian follicle, which expands proportionally. Very soon, however, and in many animals indeed from the first, fine opaque granules make their appearance, as if by precipitation or deposit, in the clearer basement substance, and thus the primitive yolk-substance of the ovum in all animals is formed. In most instances there is a time during which the ovum, consisting of germinal vesicle, with a small quantity of primitive yolk, exists, without any other covering than that given to it by the ovarian follicle; but as the deposit of the finely granular yolk increases, and at a very variable period in different animals, the vitelline membrane is formed round its exterior. The addition of this covering may be regarded as the third stage in the formation of the ovum. The manner of the origin of the vitelline membrane has not yet been accurately observed; and it is probable (as will be hereafter stated) that the coverings known under this name may have different modes of origin; but if we restrict our attention at present to such simple ova as those of Mammalia, I believe it may be stated as extremely probable that the so-called zona pellucida which constitutes the vitelline membrane of the Mammiferous ovum, takes its origin by the consodidation of the superficial part of the basement substance of the primitive yolk.

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* It has been inadvertently stated in a preceding part of this article (p. 116.) that the micropyle had not been observed in the ova of Crustacea, whereas Meissner has ascertained its presence in that of Gammarus. (See his Memoir in Zeitsch. fur Wissen. Zool. vol. v. p. 284.)

It appears probable that in the large-yolked ova, such as those of the bird, the vitelline membrane, which we find enclosing the whole mass of the yolk, owes its origin to a different source; and I am inclined to believe that in this and in many other animals the membrane which we term vitelline, as being the immediate investment of the yolk, is not of the same nature with the zona pellucida, or the simple homogeneous vesicle of the smaller ova, but rather a structure of later formation, which owes its origin to the fusion, or amalgamation, or to some other change in the outermost layer of cells which form the nutritive yolk of these animals.

In connection with this view, it is important to remark, that at that earlier stage of formation of the bird's egg when it consists entirely of formative or primitive yolk, there is an approach to the formation of a zona, in the existence of a very distinct, clear, and consistent marginal portion of the yolk blastema, from which the yolk granules seem to retire. When the large cellular or nutritive yolk is formed, this temporary zona seems to disappear, and to be replaced externally by the permanent vitelline membrane already mentioned.

In those animals in which the ovigerms arise by development within cells so as to be connected in groups (Gordiacei), and in some others, the vitelline membrane, or a substitute for it, seems to be formed from the earliest period in a different manner from that now described.

The germinal vesicle is unimacular in general in the small-yolked ova, and multimacular in the large-yolked ova, and also in the intermediate kinds. In the latter it is rare to observe the earliest stage in which the macula is still single: the multiplication of the maculæ takes place with remarkable rapidity, and apparently by a process of endogenous development, or possibly by division. The ultimate destination of these maculæ is still a subject of doubt.

3. Morphology of the ovum; homology of its parts, and relation of the ovum to other organic structures.

Should the views be correct which have now been stated with regard to the relations of the parts in the mature ovarian ovum, and the manner in which they are formed, it will be apparent that a strict homology or anatomical correspondence can be pointed out in regard only to some of the parts which are recognised under similar designations, as respectively belonging to the ova of different animals. All physiologists will probably be disposed to look upon the germinal vesicle or ovigerm as corresponding or homologous in the ova of all animals, and, notwithstanding the great differences known as to its more simple or multiple condition, the same view may also be taken of the structure known as nucleus or macula. The primitive or finely granular yolk-substance, more especially that which immediately surrounds the germinal vesicle, and is afterwards employed in the formation of the blastoderm or embryogerm, seems also to have a similar origin, structure, and relation in all animals. But beyond this it is more difficult to trace the homological correspondence; for under the names of cellular yolk-substance and vitelline membrane it appears that there have been brought together parts of which the origin, structure, and relations may be dissimilar in different animals. There seems at least to be sufficient reason, from what is already known of the varieties of the enclosing membrane, or so-called vitelline membrane, to establish a distinction between several forms of that structure; as, for example, between the vitelline membrane, which exists from the earliest period as a pediculated sac in connection with the ovarium, as in Holothuria; that which is derived from the extension of the wall of the original germ-cell in grouped ova, such as have been described by Meissner in Gordiacei; that which is later formed round the ovum of Mammalia as a zona pellucida, by the consolidation of the outer layer of the primitive basement substance of the yolk; and that which in the bird and other animals whose ova are similarly constituted, appears to derive its origin in part, at least, from coalesced cells corresponding to those of the tunica granulosa of the ovarian capsule on the exterior of the cellular yolk.

With regard to the cellular yolk itself, we must refrain from any attempt to establish its homology till we shall be more fully acquainted with the mode of its production; for it is still undetermined whether it arises by cell formation within the primitive vitelline membrane through some change in the substance of the primitive yolk, or whether it is derived, as I am inclined to believe may be the case in birds and some other animals, in a space external to these parts, and more in connection with the cellular contents of the ovarian follicle.

In limiting, then, our comparison to the parts of the ovum in a bird and a mammifer, we may regard the germinal vesicles as homologous in both; the finely granular germinal disc of the bird's ovarian egg as homologous with the whole vitellus of the mammiferous ovum; the zona pellucida of the mammiferous ovum as temporarily represented by the clear outer band of the primitive yolk, which is seen in the bird's ovarian ovum when of a diameter of from $\frac{1}{40}$ to $\frac{1}{20}$ of an inch; the cellular yolk of the bird's egg, and its enclosing vitelline membrane as probably homologous with the fluid and granular contents and lining tunica granulosa of the ovarian follicle of the mammifer, and not by any means with the corpus luteum of a later period, as has been suggested by some. The albumen of the bird's egg has its homologue perhaps in the similar deposit which the ova of several Mammalia acquire in their descent through the Fallopian tube. The chorion of the ovum of Mammalia, being an after growth, has probably no true homologue in the bird's egg, unless we should regard the shell membrane and shell as occupying this place.

Many ovologists have thought it of importance to establish a comparison between the ovum or its parts, and some one or other of those microscopic structures which, since the publication of the discoveries of Schleiden and Schwann, have been known as organised cells. Schwann himself, though looking upon the entire animal ovum as a cell, entertained some doubts as to the exact nature of the comparison to be instituted for its several parts. These doubts are not yet removed, and the progress of knowledge has tended rather to diminish than to increase the appropriateness of the comparison, more especially from the somewhat various and indefinite nature of the bodies which are now recognised as organised cells.

It cannot be denied that, if we regard merely the structure of the simpler ova of small animals, we find in them the general characteristics of an organised cell, as these have been usually understood; that is, we find the external structureless vesicular cell-wall, the internal granular contents, and the internal nucleus or inner cell with its nucleolus. But when we consider more fully the whole history even of the most simple ova, and extend our regard to the structure and history of the more complex forms of ova, we perceive many circumstances which render the comparison with detached animal cells inapplicable.

Leuckart remarks, in his article Zeugung, previously referred to (p. 815.), that if we attempt to deduce the most general result from what has been ascertained as to the formation of the ovum, it is this, that "the animal ovum is formed by deposit round the germinal vesicle." The progressive formation of the parts of the ovum, therefore, would appear to differ widely from that which Schwann held to occur in most cells. But our whole knowledge of the various forms and modes of production of cell-like structures has been extended, and has undergone some modification since the time of Schwann; and there are now known to be not a few cell structures which are formed by external deposit of matter round a nucleus, nearly in the same manner as occurs in the ovum. In this view, therefore, the simpler kinds of ova might be regarded as examples of "deposit cells."

The great variation in the magnitude of different ova, and the prodigious size which some of them attain, as compared with the minute and generally microscopic size of the organised cells of the animal body, cannot by itself be received as a conclusive argument against the cellular constitution of the ovum; but the complexity of its structure, its relation to fecundation, the peculiar micropyle of the outer wall in some, the separation of the germinal from the nutritive part of the yolk-substance, and the new formation of cells after segmentation in a limited or more extended space over the yolk in the interior of the vitelline membrane, are so widely different from any thing belonging to the history of other cells in the animal body, that we are forced to regard the ovum rather as a structure of a peculiar kind than as a mere modification of a cell.

The germinal vesicle it might be held, both in its structure and its mode of origin, merits, more justly than the whole ovum, the comparison with an organised cell. But even in its history there are points of difference, and we are still too little acquainted with the mode and consequences of its disappearance at the time of the maturation of the ovum, to warrant our making more than a vague and general comparison of the germinal vesicle to an organised cell. In admitting that the ovum, or its germinal vesicle, present some of the features of the organic cellular structure, we ought always to bear in mind that they are the source of all the other cells from which the animal body is developed.

The manner of the very first origin of the germ of the ovum is still involved in obscurity, for we only know of the existence of an ovigerm when the germinal vesicle has attained an appreciable size. Whence the first germs of the germinal vesicles proceed can as yet be matter only of conjecture. Without entering here upon the debated ground of the origin of organised cells in general *, I would venture to express the opinion, that as there is no ovigerm without a parent, so there is no new organisation without previously existing, and at some time or other connected, organisation. Hence, notwithstanding the appa-

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* See upon this subject the very interesting and suggestive Review by Mr. Huxley in the Brit. and For. Med. Chir. Review for October, 1853.

rent isolation of the origin of cells in blastema or intercellular substance, it might still be held that the unseen germs of new cells contained in that blastema may have derived their origin from other cells or organised parts proceeding from cells. And thus, in regard to the first origin of the ova of animals, it is fair to conjecture that the germs from which they spring have taken their descent from parent cells or structures derived from cells through the organs appropriate to their formation. But here observation fails to assist us further, and we are lost in the region of speculation.

If, however, with the reservations now stated, it should be thought desirable to compare the ovum to the organic cellular structures, the germinal vesicle may be regarded as the simple cell of the ovum, the whole ovum as a complex cell; the first of these being formed probably by expansion from a minute point or molecule, the second by superposition or external deposit round the internal cell; but both at the same time presenting features which are peculiar to themselves, and different from those which characterise other cells of the animal economy. The different and separate formation of the germinal vesicle and yolk, which is perceptible to some extent in the ova of most animals, is placed in its most striking point of view by those instances in which, as in Trematode and Cestoid Entozoa, there are distinct germigenous and vitelligenous organs, and those in which, as in Nematoidea and Insecta, the ovary is tubular, and the formation of the several parts of the ovum goes on progressively in different parts of the tube.

4. Phenomena attendant on the maturation of the ovum, and its discharge from the ovary.

The ovum naturally undergoes in the ovary a progressive development till it arrives at the state of maturity, when it is usually separated from the ovary by a process of dehiscence, is conducted through the female passages either to be excluded or laid, as in oviparous animals, or to be retained in a uterus or other part of the female organs in viviparous animals during uterogestation. The maturation of the ova and their separation from the ovary is in many animals periodical and independent of fecundation. This natural periodical separation of the ova has been termed *Ovulation* by some authors.*

The change which the germinal vesicle undergoes at the period of the maturation of the ovum has naturally attracted much attention, from the hope that through the observation of this phenomenon some explanation might be obtained of the first origin of the germ round which, after fecundation has taken place, the segmenting and organising stratum is collected, from which the blastoderm is produced; but it must be allowed that as yet little success has attended our efforts to detect the connection, if it exists, between these two processes. In almost all animals the germinal vesicle is lost to view at the time of the maturation of the ovum, and generally before or about the time when the ovum leaves the ovary. In large-yolked ova the maculæ of the germinal vesicle become very numerous by their multiplication and sub-division at an early period; while in the small-yolked ova, as has been observed in a few animals at least, the increase in the number of the maculæ does not take place till immediately before the diffluence or disappearance of the vesicle. The more minute phenomena of this diffluence are as yet very imperfectly known. In some animals, as Mammalia and Birds, it has been observed that shortly before the diffluence of the vesicle, its delicate wall undergoes a softening or approaching solution, so as to make it impossible to separate the vesicle entire. After this, when the diffluence is complete, the contents disappear from the situation they have previously occupied, but what becomes of them has not yet been determined. In some instances, as Birds and Batrachia, it has been observed that, after the diffluence of the germinal vesicle, the germinal part of the yolk, which previously consisted exclusively of small opaque granules, is now mingled throughout with clear hyaline spherules, somewhat similar to the dispersed maculæ of the germinal vesicle; but it is only matter of conjecture that these clear spherules have been derived from the germinal vesicle or its maculæ.

In a few instances, as in Ascaris, it has been thought that the entire nucleus or macula of the germinal vesicle has remained undivided, and it has been supposed that it has of itself constituted the germ of the embryo-cell, which afterwards occupies the centre of the first segmenting mass of the yolk, and whose progeny by division exists as nuclei in the interior of the successively increasing segments of the cleaving germinal portion of the yolk. A recent observation by J. Müller seems to lead the way to a different view of this phenomenon. He has observed * in one of the Mollusca, the Entochoncha mirabilis, that the germinal vesicle does not disappear or undergo a change at the time of the maturation of the ovum, but remains discernible as the foundation of the clear *embryonic-cell* which occupies the centre of the yolk mass when segmentation is about to take place. Remak † has been led, by his observations on the Batrachian ovum, to

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* The observations of Bischoff had long ago shown that in the periodical dehiscence of ova which accompanies the heat of female quadrupeds, the ova may be detected, though unfecundated, in the course of their descent through the Fallopian tubes and uterus (Periodische Losreifung, &c., 1842), and some observations appear also to have shown that the same is the case in the human female at the periodical return of menstruation. (See a paper by H. Letheby, M. B. in the Philos. Trans. for 1851, p. 57., where two cases are described in which ovules or their remains were detected in the Fallopian tubes of unimpregnated women who had died at or about the menstrual period.)

* Archiv. der Physiol. 1852. Leydig in the same.

† Untersuch. über die Entwickel. der Wirberthiere.

doubt the correctness of the view hitherto generally adopted as to the entire disappearance of the germinal vesicle in that instance, and holds it as probable that a part of it at least remains in connection with the formation of the embryonic cell. These statements are sufficient to show that the phenomena of the dehiscence of the germinal vesicle and its relation to the subsequent changes in the ovum induced by fecundation are as yet very imperfectly understood, and that the discovery has still to be made of the link in the chain of connection between the last stage of existence of the ovigerm, and the first origin of the nucleus round which the subsequent organising process of segmentation begins. But that some such connection exists, all who have made a study of this part of the history of the ovum are inclined to believe.

5. Relation of the ovum to fecundation by the male sperm.

The act of fecundation is necessary for the perfection of all true ova. In the production of gemmæ or buds, in the multiplication of nonsexual individuals, and in the various examples of Metagenesis previously referred to, the germs from which the new products arise may be nucleated cells or groups of these, and may without doubt be the descendants of the original cell-germs of ova; but for their development into the new beings produced from them, no combination, so far as is yet known, with the product of cells of a different kind, as in fecundation, is necessary. It is otherwise with all true ova. Their germs may be the descendants through the ovary of an original cell-germ, from which the animal bearing the ovary was produced; but for the generation of an ovum the ovigerm must be subjected to the influence of the sperm, and for its development there is required a new process of organisation, inaugurated by segmentation, which is the invariable consequence of fecundation, and is the first obvious change in a fecundated ovum leading to embryonic formation.

The developed form of the spermatic substance* is in by far the greater number of animals that of minute ovoid or rounded particles of various form, with each of which is connected a long and extremely delicate filament, which moves with vivacity in a vibrating or oscillatory manner when immersed in water and various bland animal solutions. There are other less common forms of spermatozoa, such as those of Crustacea and Nematoidea, which have not the filamentous appendage, and are motionless. The vibratory motion of filamentous spermatozoa bears some resemblance to that of some kinds of fine cilia, and is the most apparent indication of the active state of their vitality.†

It is now ascertained beyond doubt that in a number of animals the spermatozoa come into direct contact with the yolk substance and embryogerm, or with the internal contents of the ovum. The actual entrance of the spermatozoa into the ovum has been observed in Mammalia, Batrachia, Osseous Fishes, Insects, Nematoid Worms, some Mollusca, and Echinodermata; and there have been ascertained circumstances regarding the ova of other animals which warrant the inference that the spermatozoa enter the ovum in many more than those in which the phenomenon has already been actually observed. After long continued doubt and much discussion of this point, physiologists are therefore now generally agreed that in all instances a direct action of the spermatozoa in substance on the contents of the egg is necessary to fecundation. The manner of access of the spermatozoa to the interior of the ovum is probably various in different animals. In a few, as Trematode and Cestoid Entozoa, the sperm is mixed with the contents of the ovum, viz., the germinal vesicle and yolk, at the time when these are brought together from the separate organs in which they are formed: in some, as the Nematoid Worms, and probably also in some other animals, the sperm comes in contact with the ovum previous to the formation of an enveloping membrane; in a third set it seems probable that, as in Lumbricus, and perhaps in some Mollusca and Hirudinea, the vitelline membrane which had existed at an earlier period is dissolved or removed previous to fecundation, and the ovum or yolk substance and germ are thus left directly exposed to the action of the spermatozoa, which in Lumbricus have been observed in great numbers penetrating the substance of the yolk.

In the majority of animals, however, the sperm only reaches the ovum at a later stage of its formation, when it is already covered by the vitelline membrane or other envelopes, and through these coverings, therefore, the spermatozoa must pass to gain access to the yolk and germ. In a certain number of animals the vitelline or enveloping membrane appears to be quite entire and closed on all sides, so that, as in Mammalia, in which Martin Barry was the first in 1843 to perceive with certainty the entrance of the spermatozoa into the ovum, these bodies must in some way, not yet fully known, pass through the consistent wall of the enclosing membrane; but in other animals, as first discovered by J. Müller, a special aperture or perforation of the egg-covering exists, apparently destined to allow of the more rapid entrance of the spermatic bodies. This *micropyle* apparatus, sometimes consisting of one, and at others of a number of apertures, has now been observed in several Echinodermata, in Acephalous Mollusca, in all Insects, and in Osseous Fishes; and it is more than probable that it exists in a considerable number of other animals in which it has not yet been detected. But still, making due allowance for the probable extension of discovery in this direction, the care and accuracy with which the micropyle apparatus has since its first discovery been sought for without success in Mammalia and some other animals, in which, had it been present, it could scarcely have escaped so careful a scrutiny, warrant the belief that in a certain number of animals the spermatozoa do actually penetrate the apparently entire egg-covering.

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* See the article SEMEN.

† See especially the recent researches of Kölliker on the Sperm in Zeitsch. fur. Wissensch. Zool. vol. vii.

It is not my design to enter here upon the consideration of the mode and nature of the action exerted by the spermatic matter or the spermatozoa in producing the changes of fecundation. Upon this subject the reader may with great advantage and interest consult the latter part of the article Semen in this Cyclopædia by R. Wagner and Leuckart, the papers of the late Mr. Newport in several recent volumes of the Philosophical Transactions, and the learned article by Professor Leuckart on Generation contained in the fourth volume of R. Wagner's Handbuch der Physiologie. I will only remark in passing that from Mr. Newport's and other researches it appears that while the actual mixture of an appreciable quantity of the spermatic substance is necessary to induce fecundation, the extreme rapidity with which the action takes place, the minuteness of the quantity of the spermatic matter which is sufficient to induce it, and the fact now observed in a variety of instances that the spermatozoa which have entered the ovum remain apparently little changed for a considerable time after the changes of the ovum consequent on fecundation have made some progress, — lead to the conclusion that there is something in the nature of this action inconsistent with the idea that it is one of mere combination in substance of the developed contents of the male and female generative products. But whether this is to be referred to the class of "contact actions" of which themselves so little is known, or to what other kind of action it may be compared, the ascertained facts do not enable us in the least to determine. The almost universal presence of vibratory motion in the spermatozoa during the time in which they retain their fecundating power, naturally led physiologists to connect that motion with the fecundating action; but on the other hand, the occasional, though rare examples in which the spermatozoa are entirely motionless, seem sufficient to cause the rejection of the view that the force which produces the vibratory motion is identical with that which calls forth the series of histogenetic and organogenetic changes which result from fecundation.

But the consideration of this subject would lead us into the discussion of the whole question of vital forces, which in its present unsatisfactory state it is desirable to avoid. The physiologist agrees, for the sake of convenience of expression, to adopt the terms of power, property, force, &c., to denote the conditions necessary for the occurrence of certain actions or changes. He employs the term vital force merely as the indication of the supposed cause or causes of an ascertained regular sequence of vital phenomena; but all philosophical accuracy rejects the idea of any unseen separate and single force which is at work in bringing about the sequence in question. The fecundating power of the semen is an expression used only for convenience to denote the invariable sequence or relation as cause and effect which has been observed to subsist between the contact of spermatic matter with the ovum, and the changes in the latter which follow on the act of fecundation. We might with as much propriety have given a name to a separate power residing in the egg or its germ which render it susceptible of fecundation, as of a special power belonging to the semen by which that susceptibility of the ovum is acted upon. The efficient cause of the process of fecundation can only be educed, as in all physical as well as vital changes, from a perfect knowledge of all its phenomena, and the statement of the efficient cause of such actions is only the expression of the most general and best known law to which a full acquaintance with the phenomena enables them to be reduced. Fecundation is to be regarded as a purely vital change, seeing that it takes place only in the usual conditions of vitality; but, like all other vital changes, it appears more probable that a variety of conditions of the organic matter rather than any one known property or condition are necessary for its occurrence.

In endeavouring to deduce the most general phenomena which accompany this remarkable change, it may be said that fecundation consists essentially in the mutual action of two different organised bodies, which are respectively formed from two different cells; the ovigerm and the sperm-germ. If we may form any general conclusion from what may be so well observed in Nematoid Worms, the development of the ovum and the spermatic cells from their respective germs is remarkably similar, for in both the internal cell is developed from a minute molecule from within, while the external part is deposited from without. The spermatozoa are formed in connection with the nucleus or nuclei of the sperm-cell; and the germinal part of the ovum, though it consists mainly of the granular part of the yolk, which is directly formative, very probably comprehends also in some shape or other the effused contents of the germinal vesicle. In this way, then, we may conjecture that in the act of fecundation the products of the original cell-germs meet and combine or mutually influence each other. The cell-germs, then, are the links in the chain of organic connection between either or both the parents and the progeny capable of being developed from the fecundated ovum. Such a view, though still in a great measure speculative, seems to be in accordance with the facts known as to the perfect transmission of the structure and qualities of either or of both parents to the offspring.

6. Immediate effects of fecundation on the ovum; segmentation, and first changes of the ovum related to the commencement of embryonic development.

It does not come within the scope of the present article to describe in detail the process of fecundation, or the phenomena which follow it, but it may be proper to state here in a general way the relation which subsists between the earliest changes occurring after fecundation, and the commencement of those phenomena of a histogenetic nature which precede the formation of the embryo itself. The most obvious and constant of these changes is that known as the cleavage or segmentation of the yolk, — a process which has been observed in the ova of all animals, and is not less interesting from its own nature, than from the bearing of its phenomena upon the explanation of the earliest organising process of embryonic development, and upon the whole subject of histogenesis.

The segmentation affects only that part of the ovum of animals which is directly germinal or formative; and it results in the production of that layer of organised cells, of variable extent, in the centre of which, in a determinate position and direction, the rudiments of the embryo are first formed. The process of segmentation is, therefore, the prelude to the formation of the Blastoderma or germinal membrane of Pander.

The extent, therefore, to which segmentation affects the yolk differs greatly according to the amount of the yolk-substance which is directly germinal; that being in some animals the whole, and in others only a fraction of the yolk, in proportion to the part which is only indirectly nutritive. In that group of ova, then, to which those of Mammalia belong, and which we have called the small-yolked, the entire yolk, or, at all events, its superficial layer, being directly formative, or being involved from the first in the production of the Blastoderm, the segmentation is complete, or the process of cleavage affects the whole mass of the finely granular yolk within the zona or vitelline membrane. In those ova again, such as we find in the bird among vertebrate, and the cuttlefish among the invertebrate animals, in which the formative yolk has the most limited extent, and consists only of a finely granular disc near the surface of the much larger mass of the cellular nutritive yolk, the segmentation is confined to that disc alone, and is therefore, in some respects, widely different from that which occurs in Mammalia. In the intermediate group of ova belonging to Batrachia and Osseous Fishes, there are many gradations of transition from the complete to the partial cleavage, so that in some, as the common frog, it is nearly, but not entirely, over the whole yolk; while in others, as in the salmon or osseous fishes, it does not extend over more than a third of the surface of the yolk.*

In the greater number of instances there is recognised in the mass of the whole yolk, or in its germinal part, immediately previous to its undergoing segmentation, a clear simple cell, generally nucleated, which was not before perceptible; to this the name of *embryo-cell* has been given, in order to distinguish it from the germinal vesicle, from which it has hitherto been believed it is in some measure distinct. In other instances a clear spherule or space only is observed in the place of the embryo-cell, and in a few animals no clear part of this nature has yet been detected. The division of the embryo-cell accompanies, or rather immediately precedes, that of the germ-yolk, so that each mass formed by the cleavage, grooving, or segmentation, as the case may be, contains as its nucleus or centre an embryo-cell, or clear spherule of its own, descended from the first cell or spherule of the same description.

The process of segmentation, whether it involves the whole ovum, or is limited to a larger or smaller disc of the yolk, proceeds in most animals with a certain degree of geometric regularity, so that the number of germ-yolk segments are successively multiplied so as to be in the numbers 2, 4, 8, 16, 32, 64, &c., until by the ultimate division a vast number of small globular masses are formed, which occupy principally the surface of the yolk over all its germinal portion.*

The last result of the segmentation is the production of the blastoderma or germinal membrane in which, by other changes, the rudiments of the embryo subsequently make

* The more important phenomena of the yolk-germ cleavage or segmentation have been ascertained principally by the following observations: viz. 1st. of Prevost and Dumas in Batrachia, as early as the year 1824, and subsequently of Rusconi and Von Baer in the same animal; 2nd. of Bischoff and Barry in Mammalia, in 1838–39, their observations being confirmed by myself in 1840, and greatly extended by Bischoff before the publication of his work upon the development of the rabbit, in 1842; 3rd. of Bagge in 1841, and of Kölliker in 1843, on Nematoid Worms; 4th. of C. Vogt in the Salmonidæ and in the Alytes Obstetricans in 1842; 5th. of the same author, of Quatrefages, and many others in various invertebrate animals; 6th. in its most limited form the phenomenon was first well described by Kölliker in Cephalopoda in 1844; and 7th. in birds by Bergmann in 1846, by Coste in 1848, and by myself in the following years. The observations on this subject are far too numerous for quotation; those especially which have been made in experiments by artificial fecundation are most favourable to the investigation of the segmentation and other phenomena which follow immediately on fecundation. And in all these instances, as well as in very numerous others, the occurrence of segmentation and the regularity of its phenomena are so constant that we may regard it as one of the best established series of facts in organic nature. The observations with regard to segmentation in the ova of insects, which are still imperfect, form the only exception to the foregoing statement with which I am acquainted.

* Reference is here made chiefly to the best-known and most common kind of segmentation, in which this process consists in the massing of the granular and fluid substance of the yolk round the embryo-cells or clear spheres as centres; but it is right to state that there is another form of this process, as yet only observed in some of the Cestoid and Nematoid Entozoa, in which the yolk, either clear or granular in its structure, does not appear to follow the divisions of the embryo-cells, but the gradually increasing progeny of the latter assimilate or combine more and more with the yolk, so that at last, when the germinal part of the ovum is entirely occupied with new cells, the original yolk has quite disappeared. The nature of this process, as compared with the more common form of yolk segmentation, is not perhaps as yet fully understood.

their appearance. According to most ovologists, the last globules formed by segmentation are the nucleated organised cells immediately constituting the blastoderma. A different view of the process, however, in Mammalia, has been taken by Bischoff, very decidedly set forth in his two most recent works on the development of the guinea-pig and the deer; according to which the last resulting spherules formed by segmentation are not true cells, and that previous to the formation of the blastodermic cells, the yolk-germ falls completely into an amorphous or homogeneous finely granular substance, out of which, secondarily, the blastodermic cells are produced by a process of cytogenesis. It seems probable that, in the different classes of animals, there may be considerable variety in the degree of perfection in organisation or advance in cell-structure to which the segments of the yolk have attained at the period when the development of the embryo begins to manifest itself. But in the higher animals at least the weight of evidence appears to me in favour of the view that the process of segmentation results directly in the formation of blastodermic cells. The fact now established by the observations of Reichert in Entozoa, in 1841, of Ransom in osseous fishes, and more particularly those of Remak in Batrachia, that a delicate membrane is formed over the surface of each of the segments as they appear, and that the last and smallest segments possess a delicate membranous envelope, appear to show that, in these animals, each segment has the structure of an organised cell, and is very similar to, if not identical with, those of the blastodermic lamina.

The origin of the embryo-cell is still involved in obscurity. Most ovologists are disposed to connect it in some way or other with the previously existing germinal vesicle, or some part of its contents, and more especially the nucleus. For the solution of this question, as already remarked, a more accurate knowledge of what happens to the germinal vesicle at the time of that disappearance which has been so commonly observed at the period of the maturation of the ova of almost all animals, will be required. Does the macula remain, as has been alleged by some, to form the nucleus or the whole of the embryo-cell? Or, in other cases, if the multiplied maculæ are dispersed among the granules of the germinal yolk, are they again collected together into a mass or spherule to form the embryo-cell? Or, again is the embryo-cell formed out of other materials, and not necessarily either partially connected with, or wholly derived from, the germinal vesicle? And finally, might it not be, according to some recent observations, such as those of J. Müller on Entochoncha and those of Remak on the frog, that the disappearance of the germinal vesicle is not attended with the dispersion of its contents, but is a phenomenon caused only in a certain number of animals by the solution of the delicate external wall of the vesicle, and by some change in the position and consistence of its contents? Further observations will be required to determine this point; but if in the meantime we regard it as most probable that the embryo-cell is in some way or other connected in its origin with the germinal vesicle, we might further found upon this the speculative view that the blastodermic cells and the blastema from which unquestionably, by a histogenetic process of cell-division and multiplication, the various textures and organs of the animal body are produced, may be regarded as the descendants of the original cell-germ from which the ovum was developed combined with the sperm. We should thus trace the organic cellular connection between the succession of parents and offspring, which I have stated to be one of the most general facts in organised nature.

The observations respecting the very remarkable movements of the yolk, before and during the earlier stages of the segmenting process which have now been recorded by several physiologists, must excite the liveliest interest, and suggest subject for much reflection as to the evidence they may afford of the causes of this change, or, if we may use the expression, of the forces by which segmentation is brought about. There seems to be little doubt that the embryo-cell (and its nucleus first of all) is the earliest to become divided, and that the process of cleavage then proceeds from the surface of the segmenting mass inwards towards the cell; but in what relation the nucleus, granular substance of the yolk, and ovicell-membrane stand to each other in this process, must be left to be determined by future researches.

Of the other early changes in the ovum which immediately follow fecundation and precede embryonic development little need here be said. They consist principally in the greater degree of consolidation and compactness acquired by the germinal part of the yolk, and in the formation in most animals of a clear space between the surface of the yolk-substance and the enclosing vitelline membrane. It is in this clear space, or, as it has been called by Newport, respiratory chamber, that the spermatozoa have been observed in those instances in which they have been ascertained to penetrate into the cavity of the ovum. There is another phenomenon of the same period, which has now been so frequently observed, and which is of so peculiar a nature, that it must not be passed over without notice; I allude to the appearance in the respiratory space of one or more clear and highly refracting spherules, nearly of the size of the germinal vesicle, but quite independent of it. These clear hyaline-like globules have been observed in the ova of Gasteropodous Mollusca after fecundation by almost all those who have attended to the ovology of this class of animals, among whom may be mentioned Dumortier, Pouchet, Van Beneden, Nordmann, and Vogt; in the Annelida by Quatrefages; in Mammalia by Bischoff and Barry; and in Batrachia by Newport. From the observations of Quatrefages in Hermella they appear to be excluded or expressed, as it were, from the clear basement-substance of the yolk; and Bischoff states that they gradually disappear, or are dissolved without obvious change. We are at a loss to determine what office these globules may have in connection with the changes of the ovum at the time they appear.

Lastly, I would notice the interesting relation which appears to subsist between the situation of the germinal vesicle and the centre of the germinal membrane afterwards formed, or the germinal pole of the ovum, and the conformity in the direction of the line of the first cleavage of the yolk with that of the principal axis of the embryo in vertebrate animals. The first fact has been observed in all animals, and the latter has been ascertained by Mr. Newport's researches in Batrachia, and by observations which I have myself made in the bird's egg during its descent through the oviduct. These facts, as yet inscrutable in their nature, point to interesting laws relating to the connection of the first phenomena of development, which may be worked out by the further prosecution of these inquiries.

In the preceding part of this article we have considered chiefly the anatomical structure of the ova of animals, and have made little mention of their chemical composition. The knowledge of the latter subject is as yet very imperfect. In a recent Memoir* Messrs. Valenciennes and Fremy have given an account of an extended series of experimental researches in which they have been engaged, with a view to determine the differences in the chemical composition of the ova of different animals, and although this investigation is still necessarily incomplete and fragmentary, they appear already to have arrived at some interesting results. The following are some of the more important of these results.

The albumen or white is not exactly of the same composition in the eggs of different birds; but it generally contains albumen with salts and a compound of sulphur in solution. In the yolk of birds' eggs they recognise the principle first distinguished by Dumas and Cahours as *Vitelline*, a substance precipitable by mixture with a large quantity of water, and apparently more nearly resembling fibrine than albumen in its composition and some of its properties. The phosphuretted fat of the yolk is somewhat similar to the cerebral fatty matter.

The glairy white of the eggs of cartilaginous fishes is very different from that of birds' eggs, being neither soluble in water nor coagulable by heat nor acids to the same degree. It seems to contain only traces of organic matter. The angular and tabular particles of the yolk of cartilaginous fishes are composed of a principle which these authors regard as peculiar, and have named *Ichthine*. This substance is insoluble in water, alcohol, and ether, and, on being dissolved by hydrochloric acid, gives no violet colour, as albumen does. It is dissolved by all the concentrated acids, and by dilute acetic and phosphoric acids. Its composition is stated to be as follows: carb. 51; hyd. 6·7; nit. 15; ox. 25·4; phosph. 1·9.

In the ova of osseous fishes these authors do not find the same organic principle, but have detected two others in variable proportions. One of these, which they have named *Ichthidine*, exists only in small quantity, and is absent in some fishes: it is quite soluble in water. The other which is more generally prevalent and in larger though variable quantity is precipitated by water into a viscous substance. This has been named *Ichthuline*. Messrs. Valenciennes and Fremy have ascertained the interesting fact that while these principles, especially ichthuline, exist in large quantity in the ova at an early stage of their growth in the ovary, they gradually diminish in quantity or are changed as the ova approach maturity, and give place chiefly to albumen, which holds the phosphuretted fat in suspension. In the salmon's egg there is a large proportion of ichthuline, which is the cause of their becoming opaque when water enters the yolk. These authors propose indeed this character as a test of the maturity of the ova, as they are not rendered opaque by water when mature. It would be interesting to know whether fecundation produces any immediate chemical change on the principles of the yolk. The composition of ichthuline is stated to be as follows: carb. 52·5; hyd. 8; nit. 15·2; ox. 22·7; phosph. 0·6; sulph. 1.

The ova of Batrachia seem to resemble most nearly those of cartilaginous fishes, in so far that the tabular particles of the yolk are composed of ichthine. The external gelatinous covering is described as a tissue of hyaloid membrane which absorbs water in a determinate quantity.

The ova of Ophidia and Sauria resemble nearly those of birds in the composition of the white and yolk, containing the principle vitelline in the latter. The yolk of the Viper presents the singular peculiarity of becoming gelatinous by immersion in water.

In the ova of several Chelonia they have detected a different principle from vitelline to which they give the name of vitelline. This principle is soluble in potash, and has the following composition: carb. 49·4; hyd. 7·4; nit. 15·6; ox. and phosph. 26·7.

Among the invertebrate animals Messrs. Valenciennes and Fremy have examined the ova in several classes. In the Crustacea they have given much attention to the investigation of the curious colouring principle of the ova, which appears to be the same as that existing in the shell, and which being green in the moist state passes into red in a variety of circumstances. They have isolated this colouring matter by a very simple process, and give an interesting account of its properties, especially of the circumstances causing it to change to red, such as the action of alcohol, boiling, desiccation, placing in a vacuum, friction, &c.

The ova of Arachnida and Insects are

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* See Journal de Pharmacie, &c., vol. xxv. pp. 321. and 415., and vol. xxvi. p. 5., 1854.

quite different from those of Crustacea in their composition, containing albumen, fatty matters, and a large quantity of a substance precipitable by water.

The ova of Mollusca differ greatly in composition from those of other animals: more particularly in the entire absence of fat from them.

From these researches it appears that there are considerable differences in the chemical composition of the ova of animals of different great groups, and even among those not far removed from each other in the zoological scale, and that there are also considerable differences according to the state of advancement of the ova of the same animal, more especially it would appear that a marked change of composition takes place at the period of complete maturity. The researches referred to appear to have brought to light several new organic principles which are modifications of albumen or belong to the same class, and which may be considered as *Vitelline principles* as belonging to the yolk of different animals: such are Vitelline, Ichthine, Ichthidine, Ichthuline, and Emydine.

The full citations of different works and memoirs on the subjects of this article render it unnecessary to give any detailed bibliographical list at its termination. I may, however, call the attention of the reader to the following works already cited, as forming the principal basis of modern knowledge of ovology and development, viz.: The Inaugural Dissertation of *Pander* on the Development of the Chick, published in 1817. The History of the Egg before Impregnation, by *Purkinje*, in 1825. The Epistola of *Von Baer*, in 1827. The contributions of *Von Baer* and *Rathke* to *Burdach's* Physiology, in 1827 and 1828. The various Memoirs by *Rathke* at different times, and *Von Baer's* Lectures on Development, completed in 1837. The Systematic Manual of Development by *G. Valentin*, in 1835. The Prodromus and contributions by *R. Wagner*, in 1836. and the Manual of Physiology by the same author. *J. Müller's* Physiology, and especially the English translation of the more recent edition. The researches of *Martin Barry*, in 1838 and 1839. The various contributions of *Bischoff*, beginning in 1838: His Systematic Treatise on Development in 1842, and his Monographs on the Development of the Rabbit in 1842, of the Dog in 1845, of the Guinea Pig in 1852, and of the Deer in 1855. The researches of *Coste* beginning in 1833; his work on Comparative Embryology in 1837, and his large and beautifully illustrated work, as yet unfinished, beginning in 1850. The works of *C. Vogt* on the Alytes Obstetricans (Batrachia) and on the Embryology of the Salmonidæ, in 1842. Lastly, the recent and valuable researches of *Remak* on the Development of Vertebrata in 1853–1855; and the republication of *R. Wagner's* Icones Physiologicæ by *Ecker*. The works relating to the invertebrate animals are much too numerous for quotation. I will only mention the researches of *Kölliker* on the Cephalopoda, of *Quatrefages*, *Vogt*, and others on the Mollusca, Annelida, &c., and those of *J. Müller* on the Echinodermata.

I would also refer the reader to the excellent report on the progress of discovery in regard to the Ovum by *Thomas W. Jones* in the Brit. and For. Medical Review for Oct. 1843, to *Bischoff's* article on the History of Discovery in Development, and its application to the explanation of Malformations in *Wagner's* Dictionary of Physiology, to *Leuckart's* Article on Generation in the same work, and to *Vrolik's* Memoir on the Explanation of Monstrosity from the History of Development, and to his article Teratology in this Cyclopædia. A large amount of information on the whole of our subject will also be found in *C. Vogt's* interesting Letters on Living and Fossil Animals in 1851; in *Victor Carus's* System of Animal Morphology in 1853; in *Van der Hœven's* Manual of Zoology, with additions by *Leuckart* in 1850–1856; and in the English works of *Carpenter*, *Owen*, and *Rymer Jones* on Comparative Anatomy and Physiology.

In now bringing this article to a close, the author owes an apology to the conductors and the readers of this Cyclopædia for the extreme tardiness with which it has appeared. The delay has arisen, in part, from personal circumstances which need not be mentioned here, and in part from the nature of the subject of which the article treats. In the original plan of the article, it was intended that it should comprehend, along with the history of the ovum, an account of the development of the embryo. But as time advanced, and every successive year added new and important matter to our knowledge of the science, and greatly modified the statement of facts previously regarded as established, it became more and more difficult, especially in the hands of one interested in the experimental investigation of many of the individual facts, to present a systematic and at the same time clear and brief description of the researches of physiologists on the subject of development. The author regrets deeply that he should thus be prevented from furnishing the readers of the Cyclopædia with this part of the article as originally intended. But at the same time he believes that when the recent rapid progress of many departments of the subject is considered, and the vast number of details which would be required to embrace even the shortest account of the origin and formation of all the textures and organs of the animal body, the knowledge of which forms a science that is coextensive with the whole range of anatomy and physiology, it may be thought that he has in present circumstances judged rightly in abandoning the attempt to compress into a limited space the statement of so extensive and important a branch of physiological inquiry.

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